INHERITANCE OF PIGMENTATION AND POD SHAPE IN WINGED BEAN (*PSOPHOCARPUS TETRAGONOLOBUS*)

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN HORTICULTURE

MAY 1985

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ABSTRACT

The inheritance of stem, calyx, corolla, pod, and pod wing colors, as well as cross-sectional pod shape was studied. Crosses were made between 16 accessions. The F_1 and F_2 data confirmed a previous report of the dominance of rectangular to flat pod shape. For the other characters, the results were inconsistent with a simple one major gene difference as had previously been reported for stem, calyx, pod and pod wing color. A high, but variable, amount of outcrossing contributed to ambiguous results in the F_2, and rendered genetic interpretation difficult.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

The winged bean (Psophocarpus tetragonolobus) is an underexploited tropical legume, which in recent years, especially since the 1975 report by the U.S. National Academy of Sciences, has occasioned much interest by researchers as a potential major crop in the tropics. Some researchers believe it has the potential to become the most important plant protein source in the tropics. It is primarily of interest due to its unusually high protein content, high yield potential in tropical zones, and multiple use. Every part of the plant can be utilized as food. It shows potential as a green vegetable, pulse, root crop, forage, oil crop, or cover and green manure crop (Anon., 1975; Masefield, 1973; Lugo-Lopez et al., 1981; Duff, 1978; Thompson and Haryono, 1980; San Juan and Abad, 1981).

Since winged bean has such potential as a major crop and there has been relatively little work on its genetics, an inheritance study of winged bean was undertaken as a thesis project.

The primary objectives of this investigation were to determine the pattern of inheritance of certain pigmentation and pod characteristics in winged bean. These traits included pod shape and pigmentation of the stem, calyx, corolla, pod, and pod wings.

LITERATURE REVIEW

A. Taxonomy and Origin

Psophocarpus is in the subfamily Papilionoideae of the family Leguminosae. The genus *Psophocarpus*, and its 9 species have been most recently characterized and described by Verdcourt and Halliday (1978). All 9 species have more or less distinctly four-winged pods. The genus is divided into 2 subgenera, *Psophocarpus* with a stigma terminal or internal, but with hairs to the tip of the style and *Vignopsis* with the stigma terminal and hairs limited to a ring some short distance below the style tip. Subgenus *Psophocarpus* can be further divided into 2 sections, sect. *Psophocarpus* with trifoliolate leaves and sect. *Unifoliolate* with unifoliolate leaves (Fig. 1). The species most closely related to *P. tetragonolobus* are *P. scandens*, *P. palustris*, and *P. grandiflorus*. Verdcourt and Halliday suggest that *P. tetragonolobus* is either an "ennobled race of a wild species" of Asian origin now extinct or derived from *P. scandens*.

Poole (1979), however, on the basis of pollen morphology proposed a phylogenetic trend with *P. monophyllus* and *P. lecomtei* as the most likely antecedents of *P. tetragonolobus* (Fig. 2), although she states that there is no clearcut evolutionary trend evident. *P. tetragonolobus* has the most distinctive pollen and in terms of pollen

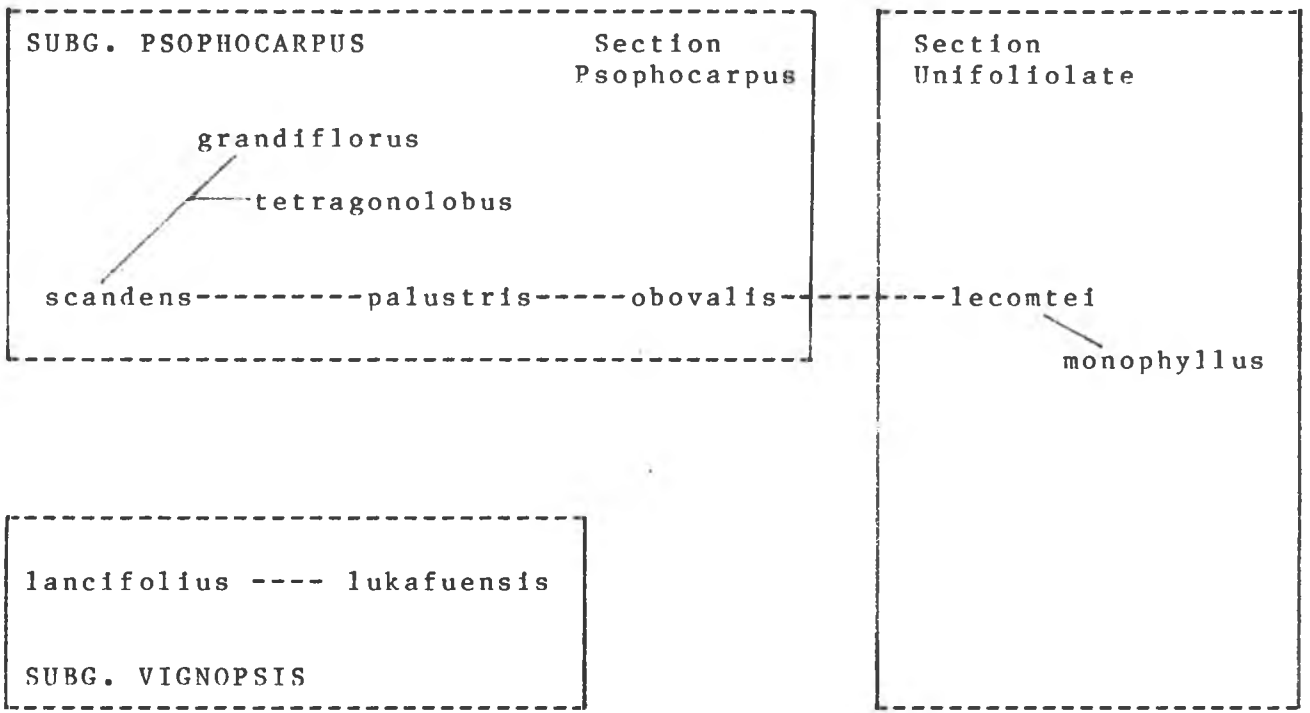

Figure 1. Classification of species of Psophocarpus (from Verdcourt and Halliday, 1978)

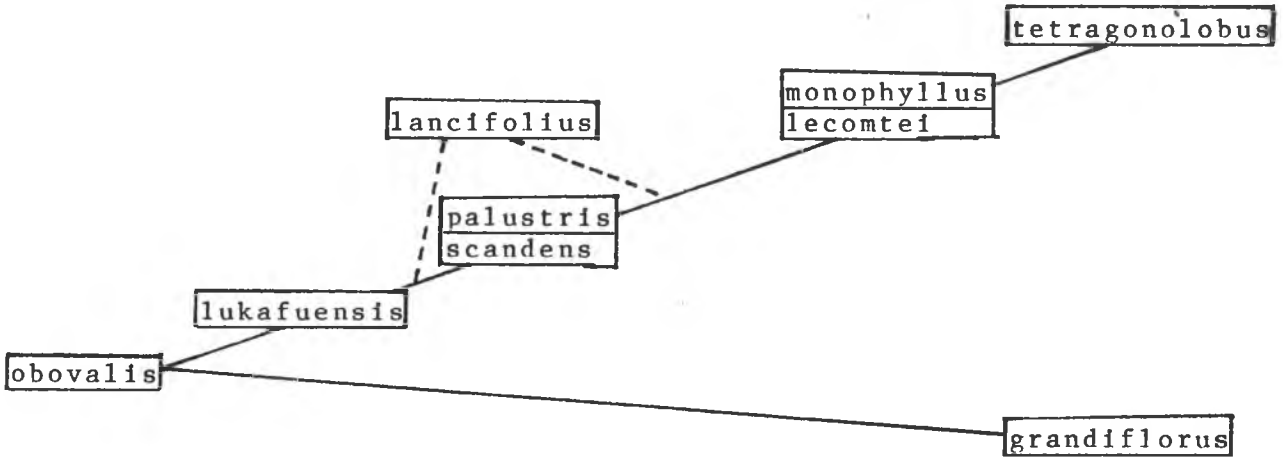

Figure 2. Proposed phylogenetic scheme (from Poole, 1979)

evolution can be considered the most specialized species.

There is no definitive evidence on the center of origin of winged bean. Determining the center of origin is complicated by the fact that P. tetragonolobus is not known in the wild state (Erskine, 1978). Africa, India, southeast Asia and Papua New Guinea have all been proposed as possible centers of origin. The winged bean, until recently, has had a largely Asiatic distribution, but there are no other Psophocarpus species found in Asia at present (Verdcourt and Halliday, 1978). All the wild species are indigenous to Africa, Madagascar, or the Mascarene Islands (Smartt, 1980), but until recent times P. tetragonolobus does not appear to have been grown there. Smartt (1980), on the basis of phytogeographical evidence, makes a case for an African origin, but with P. tetragonolobus being developed as a crop in Asia from African seed stock. Winged bean is thus a possible transdomesticate. P. grandiflorus, which is found in eastern Africa from Ethiopia through Uganda to Zaire in upland areas, is proposed as a possible ancestral species. Hymowitz and Boyd (1977) propose Papua New Guinea as a possible center of origin due to the long history of cultivation, favorability of climate and degree of diversity. Khan (1976) acknowledges Papua New Guinea to be a center of genetic diversity for winged bean and that it was cultivated there long before European contact, but discounts the possibility of winged bean being indigenous.

B. Cytology

Haq and Smartt (1977) found that the basic number of chromosomes for winged bean is 2n=18. However, they found 2n=20 in 2 accessions, one with both 2n=18 and 2n=20 samples.

Pickersgill (1980) confirmed the 2n=18 count for P. tetragonolobus and also found that P. scandens was 2n=18. In P. tetragonolobus there are 2 classes of chromosomes, with 6 short and 12 long chromosomes. The short chromosomes are all metacentric or submetacentric, whereas the long chromosomes are mostly submetacentric to acrocentric. During meiosis usually 9 bivalents are formed, although univalents sometimes occur. No evidence of structural heterozygosity was seen by Pickersgill. The short and long chromosomes may form either rod or ring bivalents. At late diakinesis or early metaphase, when the bivalents were most contracted, most chiasmata appeared to be terminal. In late metaphase, when contraction was less, subterminal chiasmata were apparently quite frequent. Thus, it is likely that chiasmata are not localized, and thus no block inheritance of genes is likely.

C. Agro-Ecology

Winged bean has been called a crop primarily adapted to the hot, humid tropics (Purseglove, 1968; Rachie and Roberts, 1974), although it has been grown in Korea at 37°37′ latitude (Kim, 1978) and in southern Switzerland under an average photoperiod of 15 hours, and temperature of 11.6 to 23°C (Ruegg, 1982).

Winged bean is also grown at higher, cooler elevations in the tropics, up to 1800 m in Malaysia, 800 m in Thailand, 2000 m in Burma (Gunasena et al., 1980-81), and up to 2400 m elevation in the Papua New Guinea highlands, although in Papua New Guinea, it is mostly grown in the valleys of the highlands at 1500-1800 m (Khan et al., 1977).

Winged bean is not generally tolerant of either drought or waterlogging. Rachie and Roberts (1974) considered 150 cm/month, well distributed, to be the minimum moisture required. This was borne out by Karikari (1978) in Ghana. Growth in the savannah areas with an average of 75 cm/year was not good, and the plants did not survive the drought period. In Papua New Guinea, winged bean is grown in the drier part of the year, June-November, but the average rainfall then is 110-210 cm/month (Khan et al., 1977). Ruegg (1981) conducted studies on induced water stress and simulated waterlogging. Water stress from day 33 to day 74 of a 172 day growth period reduced grain yields by 33% and delayed flowering 35% in one cultivar. Waterlogging, from

day 50 on, resulted in reduced leaf area, and decreased grain yield by 73-84%.

In Nigeria, winged bean was found more suitable to a humid than subhumid environment in relation to other legumes, outyielding all other legumes in the humid environment. However, winged bean yields were higher in the subhumid than the humid area, due to poor stand, waterlogging, and excessive rainfall (Nangju and Baudoin, 1979).

D. Photoperiod and Temperature Effects on Growth and Flowering

Winged bean is a short day plant. Studies by Sinnadurai (1977) in Ghana have shown that winged bean plants under long days (16 hours) failed to flower and remained in a vegetative state. Flowering, fruit set and seed yield were significantly higher under short days (8 hours), or when the dark period was broken by one hour of light at midnight than under normal daylength (12 hours). Herath and Ormrod (1979) in growth chamber experiments found that photoperiods of 14 hours inhibited flowering in all winged bean selections studied. At an 11 hour photoperiod, none of the plants flowered at 30°/25°C day/night temperature, but 17 of 20 accessions flowered at 25°/20°C. Vegetative growth and leaf area was greater at the longer photoperiod. Shoot dry matter accumulation was also greater

at 14 hours at 25°/20°C, but at 30°/25°C 7 of the 20 accessions had higher dry weight at the 11 hour photoperiod.

Eagleton et al. (1978) reported on the responses of 3 Papua New Guinean (PNG) and one Malaysian line grown in a phytotron at 10 or 12 hour photoperiods with 2 temperature combinations, 27°/22°C and 21°/16°C day/night. All lines flowered earlier under the 10 hour than the 12 hour photoperiod at the same temperatures, and all but one line flowered earlier at 27°/22°C than at 21°/16°C. The number of vegetative nodes prior to floral initiation was significantly fewer under the 10 hour photoperiod, but was less affected by temperature.

Uemoto et al. (1982) grew 11 lines, 9 from PNG, and one each from Thailand and Sri Lanka, in a phytotron under 8, 11 and 13 hour photoperiods at 20, 25 or 30°C until the third trifoliate stage, when he transferred them to a greenhouse with the natural long day, high temperature conditions of Japan in June. At the 13 hour photoperiod, at either 25 or 30°C, no flowering occurred in any lines. At 20°C, a small amount of raceme budding was observed in 2 lines, and a large amount in one line (UPS-99), but none in the other 8. At the 8 and 11 hour photoperiods responses were similar. There was more and earlier raceme budding at 20°C than at 25°C, which was better than at 30°C. It was concluded that the critical photoperiod was about 12 hours for most accessions tested. When seedlings of 4 lines were grown

first at 20°C under an 8 hour photoperiod, and then tranferred to 13, 14.5 and 16 hour photoperiods at 20 or 25°C, raceme budding ceased at an earlier node at 25°C than at 20°C. At 25°C there was no significant difference between photoperiods. However, at 20°C, for 2 lines, raceme budding continued longer at 13 than at 14.5 or 16 hours. In UPS-99, at 20°C, there was almost continuous raceme budding at all 3 photoperiods. Thus, UPS-99 is relatively photoperiod insensitive at this temperature.

There appears to be potential for developing varieties more suited to temperatures and photoperiods of temperate zones. Ruegg (1982) selected for 2 generations among PNG, Ghana, and Ivory Coast varieties for flowering at cool temperatures and then for one generation for flowering in less than 70 days. In subsequent field trials in southern Switzerland, one selection was found that flowered at 85-100 days under an average photoperiod of 15 hours and a temperature ranging from 11.6 - 23.6°C.

Wong (1981) reported that winged bean must reach a certain size or age, about 4 weeks, before flowering can be induced and then 3-4 weeks of short days are required for initiation and development of the microscopic bud stage. However, some researchers have reported time to flowering of less than 7 weeks (Pospisil et al., 1978; Haryono et al., 1978).

Thus, it is apparent that photoperiod, temperature, and photoperiod temperature interactions are involved in floral initiation. Optimal conditions for floral initiation appear to be photoperiods of less than 12 hours with temperatures around 20°C. Temperatures near the optimal can partially compensate for marginal photoperiods.

E. Flowering, Pollination and Fruit Development

The winged bean inflorescence is an axillary raceme with 3 to 12 papilionaceous flowers (Aminah-Lubis, 1978). There is a slightly curved pistil enclosed in the keel, with 10 surrounding stamens arising from the base of the ovary.

The time from sowing to flowering varies from location to location and between varieties and is related to photoperiod, temperature, and genotype, as has been previously discussed. In Indonesia, the number of days to first flowering varied from 70 to 98 days, with 84 to 144 days for 50% of the plants in each line to reach flowering (Aminah-Lubis, 1978). In Papua New Guinea, Erskine and Bala (1976) reported 43 days to flowering for the variety under study with flowering continuing over 12 weeks, but dropping off greatly after 8 weeks. In Ghana, winged bean began to flower at 46 to 61 days after sowing (Pospisil et al., 1978). In Australia at latitude 32°S the average number of days to flowering of PNG, Malaysian, and Nigerian lines planted in December or January ranged from 137 to 151 days, with an average flowering duration of 31.2 to 41.4 days.

An April planting of PNG and Malaysian lines resulted in an average of 113 to 120 days to flowering (Eagleton et al., 1978).

The winged bean flower opens during the morning usually, between 9 and 11 a.m. in Indonesia, around 9 a.m. in Sri Lanka, and between 8 and 10 a.m. in the Philippines and closes in the afternoon of the same day (Aminah-Lubis, 1978; Senanayake and Thirukethesswaran, 1978; Data and Pratt, 1980). However, flower opening in the afternoon was reported from Australia (Eagleton et al., 1978).

Anther dehiscence takes place before flower opening, variously reported as occurring between 1 and 2 a.m., 7 to 8 hours before flower opening (Aminah-Lubis, 1978), or from 8 p.m. on throughout the night prior to the day of flower opening (Senanayake and Thiruketheeswaran, 1978). Pollen viability persists for 24-48 hours at room temperature (Aminah-Lubis, 1978). Stigma receptivity has been reported as starting after anthesis (ibid), and as occurring from 26 hours before flower opening to 34 hours after, with maximum receptivity occurring during the hour just before flower opening. Pollination occurred from 9 p.m. of the day before opening until 10 a.m. of the day of flower opening (Senanayake and Thiruketheeswaran, 1978). Natural pod set is generally low in winged bean, 10-18% being usual (Erskine and Bala, 1976; Sastrapradja et al., 1980; Pospisil et al., 1978).

Under natural conditions, pollen grains start to grow 1 to 2 hours after pollination and in 2 to 3 hours are 4 to 5 times the pollen diameter in length (Aminah-Lubis, 1978). Fruit development is relatively rapid. Pospisil et al. (1978) reported that pod length increased from 38 mm at one day after flowering to 364 mm in 16 days, reaching a peak rate at days 8 to 14, with a maximum mean daily growth of 48 mm on day 8. Data and Pratt (1980), using a different line, reported that pod growth and development followed a sigmoid growth curve. Pods grew rapidly in both length and width between days 3 and 22, with a mean daily growth rate of 1.2 cm/day between day 4 and day 20, reaching a mean maximum length and width of 23.4 and 2.7 cm, respectively. Rapid growth in pod fresh weight started at day 11 until a maximum of 2.56 g/day was reached at around day 27. Seed fresh weight growth showed a diauxic growth curve, with a maximum fresh weight reached at day 45, and a decline thereafter with seed maturation and drying.

F. Cross-Pollination

Mechanisms such as anther dehiscence and stigma receptivity occurring before flower opening and the lack of reported self-incompatibility in isolated flowers would seem to indicate a high degree of selfing. However, there are so many hairs on the stigma that pollen often cannot come directly in contact with the stigmatic surface (Sastrapradja

et al., 1980). Bagging of flowers, with hand tripping, brushing, and no tripping resulted in pod set increasing from 3.33% without any tripping to 4.67 and 8.67% with hand tripping and brushing, respectively. However, open pollination had an even higher pod set of 10.67% (ibid). Senanayake and Thiruketheeswaran (1978) indicated that pod set from flowers cross-pollinated in the hours prior to flower opening was greater than from self-pollination alone. It was suggested that there was an inhibition of selfing due either to immaturity of the early pollen shed, or to an incompatibility effect which gradually diminished as flower opening approached.

Measurements of cross-pollination using stem color as a marker was done by Erskine (1980). Green and purple stemmed plants with different colored flowers were grown in alternate rows in four different environments. In 3 of the environments, less than 1% crossing was observed, whereas in the fourth, which was a lowland wet season environment, 7.6±0.9 % cross-pollination was observed. This was attributed to carpenter bees (Xylocopa aruana) which had been seen visiting the flowers. However, this is probably an underestimate, since in cowpea, for example, there has been shown to be less crossing between genotypes with different than with the same colored flowers due to the color preferences of the pollinators (Leleji, 1973). Also the closer the plants the greater the possibility of cross-pollination.

Sastrapradja et al. (1980) planted several white flowered plants amongst non-white flowered plants in 3 different plots. White flowers were said to be recessive, although no evidence was presented to support this. The percentages of detectable outcrossings were 26.1, 50, and 64.3%. The placement and number of white to non-white flowers was found to affect the percentage of outcrossing observed.

The evidence is far from conclusive concerning the amount of cross-pollination that may be encountered. However, it appears that if a suitable pollinator is present, the degree of insect out-crossing in winged bean may possibly be quite high.

G. Yield

The yield and performance of winged bean varieties seems to have a high environmental and genotype-environment component, since varieties which yield well in one locale do not necessarily perform well in others. Yields for many of the same varieties in different countries are reported by Gunasena et al. (1980-81).

The highest recorded dry seed yield that has been reported was 6.7 mt/ha in Bangladesh (Haq, 1982), with the second highest being a local variety in Malaysia, 4.5 mt/ha (Wong, 1978). In the International Winged Bean Trials, a

PNG variety, UPS-62, gave a seed yield of 4.33 mt/ha (Khan and Edward, 1981). In Australia, line UPS-45 produced 3.62 mt/ha without trellising, but with hand picking (Robertson et al., 1978).

Green pod yields of over 50 mt/ha have been reported in Sri Lanka with 3 varieties, UPS-122, TPT-2, and SLS-47 (Gunasena and Gunathilake, 1981). However in Florida, TPT-1, which had yielded 22.3 mt/ha in Sri Lanka, gave yields of only 10.76 mt/ha (Csizinsky, 1981).

Tuber yields of 17.7 mt/ha for UPS-122 and 16.0 mt/ha for Indonesian-2 were reported in Papua New Guinea (Stephenson et al., 1981; Eagleton et al., 1981). Indigenous cultivators commonly get tuber yields of over 11 mt/ha in Papua New Guinea (Khan et al., 1977). Tuber yields and seed yields tend to be inversely related, as they are competing nutrient sinks. Removal of flowers and young pods has been shown to increase tuber yields and is the standard practice in Papua New Guinea (Bala and Stephenson, 1978; Herath and Fernandez, 1978; Khan et al., 1977).

H. Diseases of Winged Bean

In the National Academy of Sciences (1975) report on winged bean, it was stated that winged bean is remarkably free of serious pests and diseases. However, since then, more and more diseases have been recorded for winged bean, although few are of economic importance. The most serious

diseases of winged bean are false rust, Pseudocercospora leaf spot, root knot nematodes, several viruses, and perhaps collar rot and powdery mildew (Price, 1978; Ravelli et al., 1978; Khan et al., 1977).

False rust, caused by Synchytrium psophocarpi, is probably the most serious winged bean disease. It has been reported from Papua New Guinea, Indonesia, Malaysia, and the Philippines (Drinkall, 1978). Yellow galls may appear on all aboveground parts of the plant, often causing malformation of pods and leaves.

A planting of 120 PNG winged bean lines showed that all but 3 were susceptible to false rust (Price, 1978). However, multiple sources of resistance have subsequently been found in Indonesian lines (Thompson and Haryono, 1979). Eight out of 43 accessions tested were classified as highly resistant, with no lesions on any plant in the line. There were also intermediate levels of resistance. All the lines exhibiting resistance tended to be late in maturity.

Resistance appears to be due to a hypersensitive reaction, with resistant plants showing necrotic flecks or lesions (Parman and Thompson, 1981). Open-pollinated progeny of resistant plants, however, showed a relatively high percentage of susceptible plants in Parman and Thompson's tests, ranging from 33 to 83%. They attributed this to a high level of cross pollination effected by bees, and concluded that resistance to false rust is recessive to susceptibility.

Probably the next in importance are the virus diseases, some of which may be the same disease under different names. In the Ivory Coast, 3 types of virus were found: ringspot mosaic virus, crincle virus, and necrotic mosaic virus (Ravelli et al., 1978). The ringspot mosaic was aphid transmitted and was mechanically transmittable. It produced plant weakening and an estimated yield loss of 10 - 29%. Crincle virus was more serious and widespread, although slow spreading. A soil borne vector, such as nematodes, or Macrodes type insects was suspected. Flowering was greatly reduced with resulting reduced pod and seed production. Several apparently immune plants were found in one accession. These plants were also morphologically distinct and had a longer vegetative cycle than the susceptible plants in the same accession. The necrotic mosaic and ringspot mosaic viruses were further characterized by Fauquet et al. (1979). The necrotic mosaic is a filamentous virus mechanically transmittable in sap from diseased plants, but is not aphid or seed transmitted. The ring spot mosaic has spherical particles with properties resembling those of a cucumovirus. It can be seed transmitted.

Cowpea mosaic virus (CMV) has been reported from both the Philippines and Brazil (Talens and Dolores-Talens, 1979; Kitajima et.al, 1979). This is characterized by mosaic and by leaf malformation.

In Indonesia, a serious problem was encountered with a yellow mosaic type virus (YMV) (Thompson and Haryono, 1979). Similar symptoms were observed in Sri Lanka and Papua New Guinea (Price, 1978). In Indonesia, 5 out of 70 accessions tested showed considerable tolerance or resistance to YMV. One of these had also shown resistance to false rust. All of the resistant accessions, except for UGM-1, tended to be late maturing. P. scandens was found to be immune to YMV as well as to false rust.

Root knot nematodes are the most widespread pest in Papua New Guinea (Khan et al., 1977). They have also been reported on winged beans in the Philippines, Mauritius, and Ivory Coast (Price, 1978; Ravelli et al., 1978). Duncan et al. (1979) screened 27 lines for resistance to both Meloidogyne incognita and M. javanica, and found all to be susceptible or very susceptible. M. incognita appears to be the more aggressive pathogen.

Leaf spot, caused by Pseudocercospora psophocarpi, is a destructive disease primarily under humid conditions. It only attacks leaves. The symptoms are small yellow spots with a whitish bloom on the undersurface. The whitish bloom becomes grey and finally black when the fungus sporulates. Price (1978) tested 120 PNG lines and found all to be susceptible. P. scandens is immune. The disease can be controlled with benzimidazole fungicides.

Other pathogens and diseases reported on winged bean are Thanetephorus cucumeris (leaf blight), Mycosphaerella sp. (concentric leaf spot), Macrophomina phaseolina, Fusarium semitectum, F. equiseti, F. moniliforme and Rhizoctonia solani (all associated with collar rot), Choanephora cucurbitum (flower blight), Colletotrichum lindemuthianum and C. truncatum (anthracnose), and Pseudomonas solanacearum (bacterial wilt) (Price, 1978; Khan et al., 1980; Fortuner and Fauquet, 1979; Abdullah, 1980; Valdez and Almodovar, 1980).

I. Variation

Winged bean exhibits a large degree of variation in biochemical, morphological and quantitative characteristics. Variation in morphological characteristics exists for leaf, pod and seed shape, as well as color of stem, corolla, pod, and seeds (Table 1). Variation in quantitative characters has also been widely observed (Haq, 1982; Sastrapradja et al., 1978; Khan and Erskine, 1978; Haryono et al., 1978; Mamicpic and Movillon, 1978). Papua New Guinea and Indonesia appear to be the areas with the greatest genetic diversity.

Erskine and Khan (1981) measured variation within and between 14 PNG land races using a total of 88 progeny. For the characteristics stem color, pod speckling, pod wing color and pod shape, an average of 80.4% of the loci were

Table 1. -- Variation in morphological characteristics[z]

Character	Reported variation
Leaf shape	deltoid, ovate, lanceolate
Stem color	green, purple, pink
Corolla	blue, white, purple, violet, pink, bluish purple
Pod color	green, lt. green, cream, purple, purplish green
Pod shape	rectangular, square, semi-flat, flat
Seed color	brown, yellow, greenish brown, purple, black, cream, white, light cream, violet, tan, beige, maroon
Seed shape	round, oval, kidney

[z]adapted from Haq, 1982

found to be polymorphic. The presence of allelic polymorphism within a land race was scored when both alleles at a locus were found amongst the plants of one land race. This was based on the assumption that there is a single gene difference between flat and rectangular podded plants, green and purple specked pods, purple and green wings, and purple and green stems. Within the land races, significant differences between families were found for time to flower, and 100 seed weight, but not for pod length. Between land races, highly significant differences were detected for time to flowering, pod length, and seed weight. Khan, in an earlier paper (1976), had reported variation in PNG lines for single leaf area, mean pod length, mean seed weight, and seed yield per plant, (Table 2). Also included are data from Indonesia showing variation among Nigerian, PNG and Indonesian accessions for mean number of seeds per pod, and from the Philippines data on variation in local accessions for seed weight, pod length, and fresh weight per pod.

J. Correlations

Examining relationships between various characters, such as yield components, and determining relative degree of genotypic variability may be useful in designing a breeding program. Table 3 summarizes simple correlations reported for various characters.

Table 2. -- Variation in winged bean quantitative characters

Character	range	mean
single leaf area (cm)[z]	19 - 459	178
mean pod length (cm)[z]	5.8 - 26.4	15.2
mean seed weight (mg)[z]	62 - 417	224
seed yld/plant (g)[z]	0.6 - 72	15.7
seed weight (mg)[y]	190 - 340	
pod length (cm)[y]	11.2 - 47.8	
fresh wt./pod (g)[y]	17.4 - 31.0	
mean no. of seeds/pod[x]		
Nigeria lines	5 - 13	
PNG "	4 - 15	
Indonesia "	6 - 12	

[z]Khan, 1976
[y]Mamicpic and Movillon, 1978
[x]Haryono et al., 1978

Table 3. -- Simple correlations between quantitative characters

Character	Correlations (+)	Correlations (-)
No. of pods	# of primary branches**[z]	pod length[z,y]
"	lvs/plant**[z]	# of seed/pod[y]
"	green pod yld**[z]	20 seed wt.[y]
"	grain yield[y]	
seed yield	shelling percentage*[x]	
"	# seeds/pod**[x]	# seeds/pod[y]
"	# of pods[y]	20 seed wt.[y]
"		pod length[y]
"		tuber yield[y]
green pod yld	length/pod*[z]	
"	wt. per pod*[z]	
pod length	wt. per pod**[x,w]	# branches*[z]
"	seed wt.**[x,w]	# lvs/plant[z]
"	# seeds/pod*[x,w]	
pod wt.	# seeds/pod*[w]	
"	100 seed wt.*[w]	

*significant at 5% level
**significant at 1% level
[z]Satyanarayana et al., 1978
[y]Khan and Erskine, 1978
[x]Khan, 1976
[w]Rajendran et al., 1978

Satyanarayana et al. (1978) in a study using 25 different varieties found a low genotypic variance for both number of pods per plant and green pod yield per plant. Genotypic variance was greatest for number of leaves per plant. Phenotypic correlations were calculated for number of leaves per plant, number of primary branches, length of pod, weight of pod, number of pods per plant, and green pod yield per plant. Green pod yield was found to be positively and significantly correlated with number of pods per plant and length of the pod, which was positively correlated with pod weight. The number of pods had a high positive correlation with number of branches and leaves per plant. This would agree with observations by Robertson et al. (1978) that vigorous varieties had more pods than less vigorous varieties. Using path coefficient analysis, it was shown that number of pods had a high direct effect and number of branches a high indirect effect on green pod yield.

Khan and Erskine (1978) growing 30 different genotypes in 5 environments, 2 in the Papua New Guinea highlands and 3 in the lowlands, found that genotypic effects were significant for grain yield, pod number per plant, seed number per pod, 20 seed weight, pod length, and shelling percentage when weighed against pooled errors. However, grain yield and pod number per plant had high coefficients of variance and were not significant against genotype X

environment variances. All significant correlations were either within the highland or within the lowland group, reflecting the differences in genotypic responses between the environments.

Pod number per plant was the only character to show strong positive genetic correlation with grain yield per plant. Number of pods per plant was negatively correlated with seeds per pod, 20 seed weight, and pod length. Seeds per pod, 20 seed weight and pod length were all strongly positively correlated. Variation in pod number was largely responsible for variation in grain yield.

Khan (1976) in an earlier study had arrived at somewhat different results with a positive significant correlation between seed yield and number of seeds per pod. Twenty seed weight was also positively, but not significantly, correlated with seed yield. This discrepancy may be due to the more precise partitioning of effects into genotypic, environmental and genotypic X environmental interaction components in the later study.

Haq (1982) also found a strong positive correlation between seed yield and pod number per plant. Harding et al. (1978) reported a positive correlation between days to harvest and seed yield.

No correlation between seed yield and protein percentage was found by Rajendran et al. (1978). Harding et al. (1978) reported a low but significant negative

correlation. However, total dry seed yield and protein production per day were very strongly positively correlated. Thus, protein yield could best be increased by increasing seed yield, with secondary selection for increased protein percentage.

K. Genetic Studies

The first reported inheritance study of winged bean was by Erskine and Khan (1977) of 5 qualitative traits in 2 crosses with 3 pure lines. They concluded that all 5 traits were controlled by single gene differences with complete dominance of purple over green in stem color, calyx color, and pod wing color. Purple specks were dominant to green pod color, and a rectangular shape pod cross-section was dominant to flat pods. The small number of parental lines used in this study should be considered before extending this conclusion to the general model.

Erskine (1981) examined inheritance of several phenological and vegetative characters in a diallel cross. Using an analysis of mean squares, he found general combining ability (g.c.a.) to be highly significant in both the F_1 and F_2 populations for time to flowering, time from flowering to maturity, leaf size, and leaf area index (LAI). In the F_1 population, g.c.a. for number of leaves per plant was highly significant. The specific combining ability (s.c.a.) was significant in the F_1 for time to flowering, and time from flowering to maturity, and highly significant

in both the F_1 and F_2 populations for leaf size. The s.c.a. was thus nonsignifcant for the F_2's in time to flowering, and time to maturity from flowering. Both the F_1 and F_2 populations had nonsignificant s.c.a.'s for LAI. Thus. it appears that for time to flowering, time from flowering to maturity, and LAI, additive genetic effects are predominant.

Narrow sense heritabilities were estimated by two procedures, a correlation of mid-parent values with the F_1 values and secondly by correlation of the F_1 with the F_2 values. High heritabilities were found only for leaf size, LAI, and time to flowering. Leaf size had heritabilities of 0.94 and 0.82, respectively, on the basis of correlation between mid-parent and F_1 and correlation of F_1 and F_2. The heritabilities for leaf area index were 0.83 and 0.74. Time to flowering had a heritability of 0.68 based on mid-parent and F_1 values, but heritability was not significant when based on the F_1 and F_2 correlations. There was a major environmental effect on number of leaves per plant and large genotype by environmental interaction for time to flowering.

Kesavan and Erskine (1978) used a non reciprocal diallel cross of 8 genotypes to examine the components of green pod yield. Yield per plot and per plant, average pod weight and number per plant, average pod length and width, pod number per plant, and time from sowing to bloom were looked at. Significant differences between populations were found for all the characters except pod number per plant. Heterosis, from both the mid-parent value and better parent,

was found for green pod yield in the F_2 population. This heterosis effect was found due to pod number per plant, since there was no heterosis for any of the other parameters.

Significant g.c.a. effects were found for yield per plot and plant, pod weight, pod length and width and time to flowering. Specific combining ability was significant for yield per plot, pod size and time to flowering. Since in all cases, the variances for g.c.a. were much higher than the s.c.a. variances, these characters are primarily under additive genetic control.

Erskine and Kesavan (1982) in a later report, again using a half diallel, again found that both general and specific combining ability were significant for green pod yield. Pod weight, length and width had highly significnt g.c.a. Pod size and weight of hybrids was largely predictable from the parental means, but yield was not. The regressions of yields of the F_2 populations onto mid-parent values were non significant, indicating the presence of non additive gene action in the genetic control of green pod yield. Thus progeny testing for yield is necessary. It was suggested that an appropriate strategy for yield improvement would involve an estimation of the g.c.a. of a wide range of genotypes by a multiple mating system. Then the genotypes with the highest g.c.a. would be crossed in a half diallel mating system in order to estimate s.c.a. effects.

MATERIALS AND METHODS

Sixteen accessions were used as parental lines of crosses in this study. These seeds were obtained from Franklin Martin of MITA in Puerto Rico, from R. de la Pena of the University of Hawaii Kauai Branch Research Station, from A.E. Thompson via H. Kamemoto, and from a local farmer (Table 4). The lines were each given a 2 or 3 symbol designation. The first letter, with the exception of UGM, which refers to its original designation, refers to the source of seed, with P for Puerto Rico, U for UH (Kauai), and H for Hawaii. The second letter, except for UGM, stands for flower color. The letters B and V indicate a violet-blue group flower, R reddish-violet, P reddish-purple, and W white.

Crosses were made to determine the inheritance of pod shape and stem, calyx, flower, pod and pod wing pigmentation. Crosses were made between parents primarily on the basis of differences in stem color, calyx color, flower color, pod color, pod wing color or pod shape. However, some parental combinations were chosen on the basis of contrasting metric traits. The combinations were limited by the availability of flowers on any particular day and by low pod set.

Crosses were made in the field at the Poamoho Experimental Farm and in a greenhouse and outdoors at the

Table 4. -- Winged bean parental lines - designations and seed sources

Original designation	Source of seed	Primary source	Study Line designation
943 (Chimbu)	MITA[z]	Papua New Guinea	PR3
951 (Ribbon)	"	Nigeria (IITA)[y]	PB5
953 (Siempre)	"	"	PB3
958 (Dual)	"	"	PV5
961 (Toano)	"	"	PB1
969	"	"	PV9
995 (Summer Pod)	"	"	PW
UPS-32	Kauai[x]	Papua New Guinea	UP3
UPS-45	"	"	UV5
UPS-47	"	"	UP7
UPS-53	"	"	UB3
UPS-62	"	"	UW2
UPS-102	"	"	UV1
UPS-122	"	"	UR2
UGM-1	A.E. Thompson	Indonesia	UGM
Local accession			HV1

[z]Mayaguez Institute of Tropical Agriculture, Puerto Rico
[y]International Institute of Tropical Agriculture
[x]from R. de la Pena

Mauka Manoa campus between September 1981 and July 1982. At Poamoho, seeds were planted approximately 1 meter apart in rows 1.5 - 2m apart. Fertilization, irrigation, and pesticide application were done by the farm crew. The vines were trained onto single strings tied between two wires, with the top wire at about 6 feet. The crossing technique used was similar to that of Erskine and Bala (1976). Flower buds were emasculated the day before opening when the keel extended beyond the calyx by at least 7 mm. The keel was slit open with forceps and all the anthers were removed by pinching off the filament. The emasculated buds were then bagged with glassine envelopes to prevent the possibility of insect pollination. The following morning these flowers were pollinated with a pollen covered stigma of a just picked open flower brushed onto the stigma of the emasculated flower. Only flowers not showing 'claw marks' from bee visitation were used as pollen sources. Pollinated flowers were rebagged until a pod started to develop, at which time the bag was carefully removed.

Progeny of some crosses previously made by Ken Taniguchi, an M.S. student in horticulture at the University of Hawaii, were also included. Four parental lines were used only by Taniguchi (PB3, PV9, UW2 and PW). Six parental lines were used by both of us (HV1, PB1, PB5, PV5, UB3 and UR2) and lines PR3, UGM, UP3, UP7, UV1 and UV5 were used only by me. The plant used by Taniguchi is designated with

an a, e.g. UB3a, and the plant or plants I used are designated b, c, d or e, unless only one plant in a particular line was used, as in all Taniguchi crosses or there were no apparent differences within the line, e.g. HV1, UGM, PV5. The characteristics of individual plants involved in successful crosses are listed in Table 5.

The F_1 and F_2 plants were all grown at the Poamoho station between November 1981 and October 1983. Each F_2 generation line was grown from open pollinated seed taken solely from one plant in an F_1 line. Seed from 2 PV5 x UV1 F_1 plants was grown out separately as F_2 lines. These were designated PV5 x UV1-a and PV5 x UV1-b.

The characters evaluated were stem color, calyx color, flower color, pod color, pod wing color, and pod cross sectional shape.

Stem color was recorded at the time of first flowers for that plant, unless flowering did not occur or was unusually late. In that case, stem color was recorded when over 90% of the plants in the field had flowered.

Stem color was initially classified on the basis of preponderance of pigmentation in the stem, with 3 categories, purple (p), purple-green (pg), and green (g). It was decided that this classification system was too subjective, as there was no clear-cut demarcation between the categories of pg and p. For the last planting of February 1983, classification was strictly on the basis of

Table 5. -- Characters of parents used in crosses

Line	Stem color[z]	Calyx color[y]	Flower color[x]	Pod color[z]	Wing color[z]	Pod shape[w]
HV1	g	g	vb	g	g	r
PB1a	g	g	vb	g	g	r
PB1b	g	g	w	g	g	r
PB3	p	g	vb	g	g	r
PB5a	g	g	vb	g	g	r
PB5b		g	vb	g	g	r
PR3	p	p	rv	p	p	r
PV5	g	g	vb	g	g	r
PV9	p	g	vb	g	g	r
PW	g	g	w	g	g	f
UB3a	p	p	vb	g	p	f
UB3b,c	p	pg	vb	p		f
UGM	g	g	vb	g	g	r
UP3a	p	p	rp	g	p	r
UP3b		p	rp	g	p	r
UP3c,d	g	p	rp	g	g	r
UP7b-e		p	rp	g		f
UR2a	p	p	rv	p	p	r
UR2b,d		p	rv	p		r
UR2c		pg	vb	p		r
UV1	p	pg	vb	g	p	r
UW2	g	g	w	g	g	f
UV5		g	vb	g		

[z] g = green, p = purple
[y] g = green, pg = purple-green, p = purple
[x] vb = violet-blue, w = white, rp = red-purple, rv = red-violet
[w] r = rectangular cross-section, f = flat

presence or absence of purpling, the same criteria used by Erskine and Khan (1977). If there was any purpling of the stem, even if only a faint tinge, it was classified as purple. Plants in earlier plantings classified as purple-green were reclassified as purple. The parental lines are listed by stem color group in Table 6.

Calyx color was classified into three groups: green (g), dark purple (p), and intermediate or purple-green (pg). Parents UV1, UB3b,c and UR2c were intermediate types, UP3, UB3a, UR2a,b,d, PR3 and UP7 were purple calyxed and all the rest were green.

Flower color, as based on color of the standard petal, was classified into 5 groups: red-purple (rp), white (wh), red-violet (rv), violet-blue (vb), and streaked (str) (Fig. 3). These groups were easily and distinctly distinguishable from each other. Parents UP7 and UP3 had red-purple flowers, PW, UW2, PB1b white flowers, UR2b and PR3 red-violet flowers and the rest had violet-blue flowers. The violet-blue group included a wide range in shade and intensity, but there was so much variability on individual plants that it was not possible to readily identify differences within this group that might be attributable to genotype.

The pod color and pod wing color were taken from the immature pod eating stage, as purpling was already evident at this stage. The pods were classified as either green (g)

Table 6. -- Stem color of parents involved in crosses

Green stemmed parents
HV1, PB1a, PB1b, PB5a, PV5, PW, UGM, UP3c,d, UW2
Purple stemmed parents
PB3, PR3, PV9, UB3a,b,c, UP3a, UR2a, UV1

a: red-purple
b: white
c: red-violet
d: violet-blue

Figure 3. Winged bean flower colors

or purple (p). Parents PR3, UB3b,c and UR2 had pods with purpling and the rest were green podded. PR3 at maturity had completely purple pods, whereas development of purple pigmentation in pods of other lines did not proceed beyond purple speckling on a green background. The pod wings were classified as either green or purple. Purple winged parents were PR3, UB3a, UP3a,b, UR2a, and UV1. The others were either green or not recorded.

Pod shape classification was based on pod cross-section. Pods were categorized as either flat or rectangular.

Statistical evaluations of the F_2 data for probability of the observed results fitting the expected genetic ratios were done with the chi-square goodness of fit test with the Yate's correction for continuity (Little and Hills, 1978).

RESULTS AND DISCUSSION

A. General Observations

1. Growth

Germination was generally good. Emergence took about two to three weeks, but in one planting (September 1982), time of emergence was very variable for one F_2 line (HV1 x UW2), with some plants coming up almost 2 months later than others.

Early growth was slow, and foliage tended to be pale green. After about a month or so of growth, the plants began to grow vigorously, with multiple branching from the base. Although all lines were indeterminate, there were different vegetative growth patterns. Some plants entered a senescent phase after seed development began, while others continued vegetative growth even with mature pods present. The production of flowers and pods also showed different patterns: a relatively concentrated period of production followed by senescence; heavy production of new flowers and pods followed by a period of relatively little flowering, and then heavier flowering again; more or less continual flower and pod production. These patterns were not seasonal, but appeared within plantings of every date.

2. Diseases

No serious diseases were observed in any of the plantings. However, in every planting, a few scattered plants showed very slow growth relative to the others. They also tended to have a paler green foliage even after the others had "greened up". In most cases they eventually greened up and grew vigorously. This has also been reported by Hildebrand et al. (1982), who found that some winged bean plants were inefficient in utilization of inorganic nitrogen and remained chlorotic until nitrogen fixation could meet the plants' nitrogen needs.

Only on senescing or senescent tissue were fungal problems observed. Pods in contact with the moist ground tended to rot if left until seed maturity.

Root knot nematodes caused quite extensive root galling on many plants (Fig. 4), but this was not evident from above-ground symptoms, as some very heavily galled plants showed very vigorous growth.

3. Insects and Mites

Insects and mites observed on winged bean were Western flower bud thrips (Thrips nigropilosis), onion thrips (Thrips tabaci), greenhouse whitefly (Trialeurodes vaporariorum), spiraling whitefly (Aleurodicus dispersus), carmine spider mites (Tetranychus cinnarbarinus), fruit bud beetles (Conotelus mexicanus), oriental rose beetles (Nezara

Figure 4. Root knot nematode symptoms on winged bean roots

viridula), pod borers (unidentified lepidoptera larvae), honey bees (Apis mellifera) and carpenter bees (Xylocopa sonorina).

Heavy whitefly infestation was common on young plants, but was not as prevalent on older plants. Spider mites were very common. Western flower bud thrips were very commonly observed inside flowers. The fruit bud beetle, a small black linear-shaped nitidulid beetle was also frequently found in the flowers. They were especially prevalent during the February 1983 planting, when almost every flower examined had one or more. They were reported by Nishida (1957) to feed on pollen and nectar, and are considered of no economic importance as a pest. Pod borers were observed only rarely and damage was minor. Rose beetles caused conspicuous damage on some plants. However, in general, only plants in a senescent phase seemed to be seriously affected.

A high degree of bee activity was observed, both of honey bees and carpenter bees. More bees of both species were observed on the winged bean plants in the summers of 1982 and 1983 than during other times of the year. It could be determined from looking at the flowers whether or not they had been visited, as "claw marks" were left by honey bees on the wing petals, and carpenter bees severely tore up the petals. During the summers of 1982 and 1983, virtually every flower showed claw marks. Although Erskine (1980)

concluded that honey bees are not effective pollinators of winged bean and attributed cross-pollination in Papua New Guinea to carpenter bees, Xylocopa aruana, a species closely related to the one found in Hawaii, I have observed honey bees work open the keel and expose the stigma. They also collect pollen in the pollen sacs on their legs. Thus, it appears that honey bees may possibly do some cross-pollination. Although carpenter bees were less abundant than honey bees, both were present and may have been transferring pollen.

4. Pollination and Pod Set

There was a low rate of pod set in all the plantings. Overall, I estimate that about 10% of flowers set pods. Less than 10% of pollinated emasculated flowers set pods, as most flowers dropped within a few days of pollination. All emasculated flowers which were left un-pollinated failed to set pods.

Fifty-one supposed crosses yielded seed and were grown out as F_1's, with 18 of these being continued on to the F_2 generation. The characteristics of the parental lines in each successful cross are listed on a cross by cross basis in Table 50 in the Appendix.

B. Crosses Exhibiting Only Maternal Traits

Six crosses showed only traits of the maternal parent in the supposed F_1 and F_2 generations (Table 7). Segregation for traits in which the parents differed did not occur in what was supposedly the F_2 generation. These 6 families probably resulted from inadvertent self-pollinations. All of the apparent selfs were from crosses made by Ken Taniguchi. Taniguchi (personal communication) indicated that he may have squeezed the anthers during emasculation, possibly forcing out pollen and causing accidental self-pollination. Another possibility may be that he emasculated buds in which the anthers had already dehisced. I observed that pollen is sometimes shed the day before flower opening rather than the night before as is usually the case. Other supposed F_1's from Taniguchi crosses may also be inadvertent selfs. However, it is not possible to positively identify these without growing out the F_2.

Table 7. -- F_2 populations not showing variability that was expected

Population	Stem color[z]	Calyx color[y]	Flower color[x]	Pod color[z]	Wing color[z]	Pod shape[w]
HV1 x PW	g=59 p=14	g=73	vb=73[v]	g=73	g=73	r = 72[v] f = 1
HV1 x UW2	g=36 p= 4	g=40	vb=39[v] stk= 1	g=39 p= 1	g=40	r = 40[v]
PB5a x PW	g=54 p=12	g=65 pg= 1	vb=65[v] w= 1	g=64 p= 2	g=66	r = 66[v]
PV5 x UB3a	g=52[v] p=17	g=69[v]	vb=69	g=69	g=69[v]	r = 69[v]
PV5 x UP3a	g=72[v] p= 2	g=74[v]	vb=74[v]	g=74	g=74[v]	r = 72 f = 2
PV5 x UW2	g=74 p= 3	g=77	vb=77[v]	g=77	g=77	r = 77[v]

[z]g = green, p = purple

[y]g = green, pg = purple-green

[x]vb = violet-blue, stk = streaked, w = white

[w]r = rectangular pod cross-section, f = flat pod

[v]trait expected to show segregation in F_2

C. Uniformity and Variability in Parental and F_1 Lines

Fourteen out of 16 parental lines showed variability for one or more traits (Table 8). Possible causes of this variability are environmental non-genetic factors, mixtures of homozygotes within some parental lines, or heterozygosity in the parents.

Environmentally induced variability is unlikely here because Erskine and Khan (1977) have reported that stem color, calyx color, pod color, wing color and pod shape were qualitative traits under genetic control, and in most cases parents passed on their traits to their progeny.

If the parental line variability is due to a mixture of homozygotes, then F_1's between any two homozygotes should still be uniform. However, 19 out of 45 F_1 lines showed variability for at least one trait (Table 9). Since many F_1's show variability, this suggests that many of the parents were heterozygous or there was considerable foreign pollen contamination. Pollen contamination could be due to either pollen transfer to the emasculated bagged flowers by thrips or fruit bud beetles or pollen contamination, by insects, of the opened flowers used as pollen sources. Thus, the pollen would be a mixture of the intended pollen and foreign pollen. Although thrips and fruit bud beetles were observed inside bagged flowers, it is not thought that they were transferring pollen from plant to plant, because there were large numbers of F_1's without variability and

Table 8. -- Winged bean parental lines - range of characters

Line	Stem color[z]	Calyx color[y]	Flower color[x]	Pod color[z]	Wing color[z]	Pod shape[w]
HV1	g	g	vb	g	g	r
PB1	g, p	g	vb, w	g	g	r, f
PB3	g, p	g, pg	vb	g, p	g	r
PB5	g, p	g, pg	vb, w	g, p	g	r
PR3	p	p, g	rv, vb	g, p	g, p	r
PV5	g, p	g	vb	g	g	r
PV9	p	g, pg	vb	g, p	g	r, f
PW	g	g	w, vb	g	g	f
UB3	p	pg, p	vb, rp	g, p	p	r, f
UGM	g	g	vb	g	g	r
UP3	g, p	p, g	rp, vb	g	g, p	r
UP7	p, g	p, g	rp, vb	g	g, p	r, f
UR2	p	p, pg	rv, vb	p	p	r
UV1	p, g	pg, p	vb	g	p	r
UW2	g	g	w, vb	g	g	r, f
UV5	g, p	g, p	w, vb, rv	g	g, p	r, f

[z] g = green, p = purple
[y] g = green, pg = purple-green, p = purple
[x] vb = violet-blue, w = white, rp = red purple, rv = red violet
[w] r = rectangular pod cross-section; f = flat

Table 9. -- Range of characters in F_1 crosses

Cross	Stem color[z]	Calyx color[y]	Flower color[x]	Pod color[z]	Wing color[z]	Pod shape[w]	n[v]
Uniform F_1's with F_2 progeny[u]							
HV1 x PB5a	g	g	vb	g		r	5
PB3 x PV5	g	g	vb	g		r	5
PV5 x PB5a	g	g	vb	g		r	5
PV5 x UV1	g	g	vb	g	g	r	4
UV1 x PV5	g (?)	g	vb	g	g	r	4
UGM x PB1b	g	g	w	g	g	r	6
UR2b x PB1b	p	g	w	g	g	r	4
Nonuniform F_1's with F_2 progeny							
PB3 x PW	g,p	g	w	g		r	5
PB5b x UP7c	g	p	rp	g,p	g	r	4
UB3a x HV1	g,p	pg,p	rp,vb	g,p		r	2
UGM x UB3b	p	g,pg	vb	g	g	r	9
UV5 x UP3b	g	g,pg,p	rp,vb	g	g,p		5

See footnotes, p. 50

Table 9. (cont.). Range of characters in F_1 crosses

Cross	Stem color[z]	Calyx color[y]	Flower color[x]	Pod color[z]	Wing color[z]	Pod shape[w]	n[v]
Uniform F_1's without F_2 progeny							
HV1 x PR3c	p	pg	vb	p	g	r	4
HV1 x UGM	g	g	vb	g	g	r	4
HV1 x UP3c	p	g	vb	p	g	r	4
HV1 x UW2	g	g	w	g	g	r	5
PB1a x UW2	g	g	w	g		r	5
PB5a x HV1	g	g	vb	g		r	4
PB5b x UP7b	p	p	rp	g	p		4
PV5 x HV1	g	g	vb	g		r	3
PV5 x PB3	p	g	vb	g		r	5
PV9 x UB3a	p	p	vb	g	p	f	5
PW x HV1	g	g	w	g		r	4
PW x PB1[s]	g	g	w	g		f	4
PW x PB3[s]	g	g	w	g		f	5
PW x UW2	g	g	w	g		f	5
UGM x HV1	g	g	vb	g	g	r	3
UGM x UB3c	p	pg	vb	p	g	r	2
UV1 x PR3b	p	p	vb	p	p	r	4
UW2 x PB5a	g	g	w	g		r	3
UW2 x UB3a	p		vb	g		f	5

See footnotes on next page

Table 9. (cont.). Range of characters in F_1 crosses

Cross	Stem color[z]	Calyx color[y]	Flower color[x]	Pod color[z]	Wing color[z]	Pod shape[w]	n[v]
Nonuniform F_1's without F_2 progeny							
HV1 x PR3b	p	pg,p	vb	p	g	r	4
PB1a x HV1	g	g	vb	g		r,f	5
PB3 x HV1	p,g	g	vb	g		r	5
PB3 x PB1a	p,g	g	vb	g,p		r	5
PB3 x PB5a	p,g	g	vb,str	p		r,f	5
PB3 x UB3a	p,g	p	rp,vb	p	p	r,f	5
PB3 x UR2a	p,g	p,pg,g	vb	p,g	p,?	r	10
PB3 x UW2	p,g	g	w	g			5
PV5 x PB1a	g	g	vb	g		r,f	2
PW x UB3a	p,g		vb	g		f	4
UGM x UP3d	g	g,p	vb,rp	p,g	g	r	4
UGM x UR2d	p,g	pg	vb	g	g,p	r	5
UP7d x UR2c	p,g	p	rp,vb	g	g,p		5
UP7e x UR2c	g	p	rp	p	g,p	r	4

[z] g = green, p = purple
[y] g = green, pg = purple-green, p = purple
[x] vb = violet-blue, w = white, rp = red-purple, str = streaked
[w] r = rectangular cross-section, f = flat cross-section
[v] number of plants in F_1 planting
[u] selfs from Table 7 not included
[s] possible self

Nishida (1957) reported that fruit bud beetles were not effective pollinators. Flowers visited by bees had observable tears or scratches on the petals and were not used as pollen sources.

There were 3 F_1's with traits which had not been observed in either parental line: PB3 x PB5a for flat pod shape, and HV1 x UP3c and UGM x UP3d for speckled pods. These 3 F_1's may result from foreign pollen contamination. This does not include F_1 lines with purple-green calyxes if both purple and green calyxes were observed in the parental lines, since at this point the possibility of purple-green being an expression of a heterozygote of a green by purple cross can not be excluded. Including purple-green calyxes, there would be 6 crosses listed. All other F_1 lines had only traits which were present in one or both of the parental lines. Thus, F_1 variability can be explained in almost every case by variability in the parental lines.

The only parental lines uniform for every character examined were UGM and HV1. In addition PV5 was uniform for all traits except stem color. All PV5 plants were green except for one purple stemmed plant recorded by Taniguchi. PV5 can be assumed to be homozygous for traits other than stem color. Line PW was uniform for all recorded characters except flower color, but only one plant was used as a parent and the F_1 lines were each uniform for flower color. These 4 parental lines can be used as test lines in crosses with

individuals of other lines to determine whether the latter are heterozygous or homozygous for a particular trait. Heterozygous parents can be detected when the F_1 generation shows variability. Nine crosses with tester lines showed variability in the F_1 (Table 10), indicating heterozygosity in 6 parents as listed in Table 11. The cross UB3a x HV1 suggested heterozygosity in 4 traits for UB3a, but this was not supported by the other crosses in which UB3a was a parent. Thus, UB3a x HV1 may be another contaminated pollen cross.

If the selfs, listed in Table 7, and the 3 contaminated crosses (PB3 x PB5a, HV1 x UP3c and UGM x UP3d), are excluded from further consideration, the remaining lines can be evaluated for traits in which the F_1 was uniform. The parental lines which in crosses with a tester line gave variable F_1's suggest that the parent was heterozygous for that trait (Table 11). Seven crosses between parents not differing for any characters gave uniform F_1's (Table 12). The crosses which are expected to segregate in the F_2 because their parents differ for at least one character are summarized in Table 13.

Table 10. -- Crosses with tester lines showing variability in the F_1

Tester Line	F_1 Crosses Showing Variability
UGM	UGM x UB3d, UGM x UR2d
HV1	HV1 x PR3b, UB3a x HV1, PB1a x HV1, PB3 x HV1
PV5	PV5 x PB1a
PW	PB3 x PW, PW x UB3a

Table 11. -- Traits showing variability in the F_1 in crosses with tester lines

Parental Line	Trait Showing Variability
PB1a	pod shape
PB3	stem color
PR3b	calyx color
UB3a	stem color
UB3d	calyx color
UR2d	stem color, pod wing color

Table 12. -- Uniform crosses between parents not differing for any recorded traits

HV1 x PB5a, HV1 x UGM, PB5a x HV1, PV5 x PB5a, PV5 x HV1, UGM x HV1, PW x UW2

Table 13. -- F_1 variability, parental differences and lack of differences in crosses[z]

Cross	Stem color	Calyx color	Flower color	Pod color	Wing color	Pod shape
HV1 x PR3b	d	x	d	d	d	s
HV1 x PR3c	d	d	d	d	d	s
HV1 x UW2	s	s	d	s	s	d
PB1a x HV1	s	s	s	s	s	x
PB1a x UW2	s	s	d	s	-	d
PB3 x HV1	x	s	s	s	s	s
PB3 x PB1a	x	s	s	x	s	x
PB3 x PB5a	x	s	s	s	s	x
PB3 x PV5	x	s	s	s	s	s
PB3 x PW	x	s	d	s	s	d
PB3 x UB3a	x	d	x	s	d	x
PB3 x UR2a	x	x	d	x	d	s
PB3 x UW2	x	s	d	s	s	d
PB5b x UP7b	-	d	d	s	-	d
PB5b x UP7c	-	d	d	x	-	d
PV5 x PB1a	s	s	s	s	s	x
PV5 x PB3	x	s	s	s	s	s
PV5 x UV1	d	d	s	s	d	s
PV9 x UB3a	x	d	s	s	d	d

See footnotes on next page

Table 13. (cont.). F_1 variability, parental differences and lack of differences in crosses[z]

Cross	Stem color	Calyx color	Flower color	Pod color	Wing color	Pod shape
PW x HV1	s	s	d	s	s	d
PW x PB1a	s	s	d	s	s	x
PW x PB3	x	s	d	s	s	d
PW x UB3a	x	d	d	s	d	s
UB3a x HV1	x	x	x	x	d	d
UGM x PB1b	s	s	d	s	s	s
UGM x UB3b	d	x	s	d	-	d
UGM x UB3c	d	d	s	d	-	d
UGM x UP3d	s	x	x	x	s	s
UGM x UR2d	x	d	d	d	x	s
UP7d x UR2c	x	d	x	d	x	d
UP7e x UR2c	s	d	d	d	x	d
UR2b x PB1b	-	d	d	d	-	s
UV1 x PR3b	s	d	d	d	s	s
UV1 x PV5	d	d	s	s	d	s
UV5 x UP3b	-	x	x	s	x	-
UW2 x PB5a	s	s	d	s	s	d
UW2 x UB3a	x	d	d	s	d	s

[z]selfs and contaminated crosses excluded

d = parents differing for trait
s = parents same for trait
x = F_1 variable for trait or indication of heterozygosity for trait in a parent

D. Characters in F_1

1. Stem Color

All crosses between green stemmed parents, (excluding contaminated crosses), gave green stemmed F_1's (Table 14), which is consistent with green being homozygous recessive as has been reported by Erskine and Khan (1977). Crosses between purple stemmed parents gave purple F_1's in cases with uniform F_1's (Table 15).

Crosses between purple and green stemmed parents for which the F_1 line was uniform gave purple stemmed F_1's, except for PV5 x UV1 and UV1 x PV5 (Table 16). The validity of the stem color evaluation of the F_1's of PV5 x UV1 and especially UV1 x PV5 is questionable. The UV1 stem phenotype was very faintly purpled and the purple stemmed F_2's were also very faintly purpled. The F_1's for UV1 x PV5 and PV5 x UV1 were recorded as green, but this may have been a mistake in evaluation. There was a change in evaluation procedure for this trait as has been discussed in Materials and Methods. This could have led to some discrepancies in classification, especially the classification of some plants as green stemmed which would have been classified as purple under the later classification. However, very few plants showed such slight stem purpling.

Thus, on the basis of the F_1 data, green stem color appears to be recessive to purple.

Table 14. -- Stem color of F_1's - crosses between green stemmed parents

Cross	F_1 stem color[z]
HV1 x PB5a	g
HV1 x UGM	g
PB1a x HV1	g
PB1a x UW2	g
PB5a x HV1	g
PV5 x HV1	g
PV5 x PB1a	g
PV5 x PB5a	g
PW x HV1	g
PW x UW2	g
UGM x HV1	g
UGM x PB1b	g
UW2 x PB5a	g

[z] g = green

Table 15. -- Stem color of uniform F_1's - crosses between purple stemmed parents

Cross	F_1 stem color[z]
PV9 x UB3a	p
UV1 x PR3b	p

[z] p = purple

Table 16. -- Stem color of uniform F_1's - crosses between green and purple stemmed parents

Purple stem	Green stem	F_1 Stem Color[z]
PR3b	HV1	p
PR3c	HV1	p
UB3a	UW2	p
UB3b	UGM	p
UB3c	UGM	p
UV1[y]	PV5	g (?)
UV1[x]	PV5	g
[w]PB3[y]	PV5	g
[w]PB3[x]	PV5	p

[z] p = purple, g = green
[y] maternal parent in cross with PV5
[x] paternal parent in cross with PV5
[w] parent apparently heterozygous, see Table 11

2. Calyx Color

Crosses between green calyx parents gave green calyx F_1's in every case (Table 17).

Two crosses between the green calyx PV5 and the purple-green calyx UV1 gave green calyx F_1's, but crosses between the purple-green UB3 and the green UGM gave either purple-green calyx or both purple-green and green calyx F_1's (Table 18). The crosses between purple-green and purple calyx parents gave purple calyx F_1's.

In crosses between purple and green calyx parents, UP7 was the only purple parental line which gave consistent F_1 results, giving only purple F_1's in 2 crosses with PB5 (Table 19). The F_1 results for the other purple calyx parental lines, UB3a, UP3b, UR2a,b,d and PR3 are very variable. This may be partly due to heterozygosity in the parents, but the results are not readily interpretable, especially the presence of all 3 phenotypes in some progeny.

Table 17. -- F_1 calyx color - Crosses between 2 green calyx parents

Cross	F_1[z]
HV1 x PB5a	g
HV1 x UGM	g
HV1 x UW2	g
PB1a x HV1	g
PB1a x UW2	g
PB3 x HV1	g
PB3 x PB1a	g
PB3 x PV5	g
PB3 x PW	g
PB5a x HV1	g
PV5 x HV1	g
PV5 x PB1a	g
PV5 x PB3	g
PV5 x PB5a	g
UGM x HV1	g
UGM x PB1b	g

[z] g = green calyx

Table 18. -- F_1 calyx color - crosses between purple-green and green or purple calyx parents

Purple-green parent	Green parent	F_1[z]
UV1[y]	PV5	g
UV1[x]	PV5	g
UB3b	UGM	g, pg
UB3c	UGM	pg
	Purple parent	
UV1	PR3b	p
UR2c	UP7d,e	p

[z] g = green, pg = purple-green, p = purple
[y] paternal parent
[x] maternal parent

Table 19. -- Calyx color - F_1's of crosses between green and purple calyx parents

Purple parent	Green parents	F_1[z]
UB3a	HV1	pg, p
"	PB3, PV9	p
PR3b	HV1	pg, p
PR3c	HV1	pg
UR2a	PB3	g, pg, p
UR2b	PB1b	g
UR2d	UGM	pg
UP7b	PB5b	p
UP7c	PB5b	p
UP3b	UV5	g, pg, p

[z] g = green, pg = purple-green, p = purple

3. Flower Color

All crosses between violet-blue parents gave violet-blue F_1's (Table 20).

Crosses between a white flowered parent and a violet-blue parent gave white flowered F_1's in every case, except two (Table 21). In 2 crosses between UB3a and a white flowered parent the F_1 was violet-blue. Since the violet-blue group included a range of flower colors, it is possible UB3a has a different genotype than the other violet-blue parents. Although the UB3a violet-blue phenotype was dominant to white flowers, in all the other crosses, white was dominant to violet-blue.

Two crosses between red-purple UP7 and violet-blue PB5b gave red-purple progeny (Table 22), indicating dominance of red-purple to violet-blue. The cross between red-purple UP3b and violet-blue UV5 gave red-purple and violet-blue flowered plants in the F_1, so UP3b was apparently heterozygous for flower color.

Crosses with the red-violet flowered parents UR2 or PR3 gave an F_1 with flowers the same color as the other parent in every case (Table 23). Red-violet appeared to be recessive to violet-blue, white and red-purple.

Table 20. -- F_1 flower color - crosses between violet-blue parents

Cross	F_1[z]
HV1 x PB5a	vb
HV1 x UGM	vb
PB1a x HV1	vb
PB3 x PB1a	vb
PB3 x PV5	vb
PB5a x HV1	vb
PV5 x PB1a	vb
PV5 x PB3	vb
PV5 x PB5a	vb
PV5 x UV1	vb
UGM x HV1	vb
UGM x UB3b,c,d	vb
UV1 x PV5	vb

[z]vb = violet-blue flower color

Table 21. -- F_1 flower color - crosses between white and violet-blue parents

White parent	Crosses with vb parent	F_1[z]
PW	PB3 and HV1 (twice), PB1a	w
UW2	PB3, PB5a, HV1	w
PB1b	UGM (twice)	w
PW	UB3a	vb
UW2	UB3a	vb

[z]w = white, vb = violet-blue

Table 22. -- F_1 flower color - crosses between red-purple and violet-blue parents

Red-purple parent	Vb parent	F_1[z]
UP7b	PB5b	rp
UP7c	PB5b	rp
UP3b	UV5	rp, vb

[z]rp = red-purple, vb = violet-blue

Table 23. -- F_1 flower color - crosses with red-violet parents

Red-violet parent	Red-purple parent	F_1
UR2c	UP7d	rp, vb
UR2c	UP7e	rp
	White parent	
UR2b	PB1b	w
	Violet-blue parent	
PR3b,c	HV1	vb
PR3b	UV1	vb

[z]rp = red-purple, vb = violet-blue, w = white

4. Pod Color

Three purple pod parental lines gave variable F_1 results from crosses with green parents (Table 24). In 4 crosses with green pod parents, PR3 gave purple pod F_1's. In 4 crosses, UR2 gave green pods and UB3 in 3 crosses gave both green and purple pod F_1's. Thus, purpling appears to be dominant in PR3 crosses, but recessive in UR2 crosses. Since the PR3 phenotype is distinctly different from the other purple pod phenotypes (the whole pod eventually turns a deep red purple, whereas pod pigmentation in the other lines doesn't progress beyond purple speckling), these are apparently under different genetic control.

Although green by green crosses gave green pod F_1's in most cases, some crosses between green pod parents gave purple speckled pod F_1's (Table 25). If this is a one gene trait and purpling is dominant as Erskine and Khan (1976) contend, then for purpling to show up in the F_1, purpling would have to be expressed in one of the parents. If green is dominant, then purpling would show up in the F_1 only if both parents were heterozygous for this trait. If these results are due to genetic reasons, it seems that more than one locus is involved and that epistasis or complementary gene action is probably accounting for purpling occurring in the F_1 of crosses between green podded plants.

Another explanation for this is reduced or incomplete penetrance of the gene or gene combination for purpling thus

Table 24. -- Pod color of uniform F_1's - crosses between purple and green parents

Purple parent	Green parents	F_1 pod color
UR2b	PB1b	green
UR2c	UP7d	green
UR2d	UGM	green
UR2e	UP7	green
PR3	UV1, PB3, HV1 (twice)	purpling
UB3b,d	UGM	green
UB3c	UGM	purpling

Table 25. -- Crosses between green pod parents with purpling in pods of F_1's

Parent from parental line with purpling	Green parent	F_1 pod color[z]
UB3a	HV1 (twice)	g, p
PB5b	UP7c	g, p
PB3	PB1a	g, p
Both parents from parental line with purpling		
PB3 x UB3a		p

[z] p = purpling, g = green

expression of purpling may be due to both genotype and the environment.

5. Pod Wing Color

Crosses between green winged parents gave green pod wings in every recorded case (Table 26).

Crosses between purple and green winged pods gave green pod wing F_1's, except for 2 crosses with PB3 as the green wing parent (Table 27). Since pod wing color wasn't recorded for all the parents and F_1's, there is not sufficient data to draw any definite conclusions.

6. Pod Cross-sectional Shape

Crosses between rectangular pod parents gave rectangular pod F_1 progeny in all cases with uniform F_1's (Table 28). Crosses between flat podded parents gave flat podded F_1's in all 3 cases.

Crosses between flat podded and rectangular podded parents gave rectangular F_1's in 10 out of the 11 crosses with uniform F_1's (Table 29). Cross PV9 x UB3a had flat podded F_1's. However, parental line PV9 also had flat podded plants in it, suggesting the parent used may have been heterozygous for pod shape. So, pod rectangular cross-section appears to be dominant to flat pod shape.

Table 26. -- F_1 pod wing color - crosses between parents with similarly pigmented pod wings

Cross	F_1 Pod Wing Color[z]
Green Pod Wing Parent Crosses	
HV1 x UGM	g
HV1 x UW2	g
UGM x HV1	g
UGM x PB1b	g
Purple Pod Winged Parent Cross	
UV1 x PR3b	p

[z] g = green, p = purple

Table 27. -- F_1 pod wing color - crosses between purple and green winged parents

Purple wing	Green wing	F_1[z]
UB3a	HV1, UW2	g
UB3a	PB3	p
UV1	PV5 (twice)	g
PR3b,c	HV1	g
UR2a	PB3	p

[z] g = green, p = purple

Table 28. -- F_1 cross-sectional pod shape - crosses with similar pod shape parents

Maternal parent	Paternal parents	F_1[z]
Crosses Between Rectangular Parents		
HV1	PB5a, PR3b, PR3c, UGM	r
PB3	HV1, PB1, PV5, UR2a	r
PB5a	HV1	r
PV5	HV1, PB3, PB5a, UV1	r
UGM	HV1, UR2d	r
PB1a	HV1	r, f
PV5	PB1a	r, f
Crosses Between Flat Parents		
PW	UB3a, UW2	f
UW2	UB3a	f

[z] r = rectangular, f = flat

Table 29. -- F_1 cross-sectional pod shape - crosses between rectangular and flat podded parents

Flat pod parents	Rect. pod Parents	F_1 [z]
UB3a	PV9	f
UB3b,c,d	UGM	r
UP7c	PB5b	r
UP7e	UR2c	r
PW	PB3 (2x), HV1 (2x)	r
UW2	PB5a, PB1a, HV1	r

[z] r = rectangular pod cross-section; f = flat pod

E. Characters in F_2

Since each F_2 family was derived from one F_1 plant, the ratios should be normal F_2 ratios regardless of whether the F_1 arose from homozygous or heterozygous parents. Thus, each locus which is heterozygous should segregate and each locus which is homozygous should not. The traits for which segregation is expected, based on differences between the parents, are listed in Table 30.

Apart from the selfs, the only instances in which a cross between 2 parents with a differentiating trait did not show segregation in the F_2 were PB3 x PW for stem color and UGM x UB3b for pod shape (Table 31). This is not surprising for PB3 x PW because, as noted earlier, PB3 was heterozygous for stem color. Since the F_1 data suggest purple is dominant to green, a green stemmed F_1 plant such as the F_1 parent, should be homozygous recessive for that locus. Similarly, UB3b may have been heterozygous for pod shape.

In some F_2 lines, there were plants with characters not reported for either parent or the F_1 (Tables 32 and 33). These were defined as off-types. A possible explanation for their occurrence is outcrossing in the F_1. There was much carpenter bee and honey bee activity observed. The large amount of heterozygosity in the parental lines also implies that outcrossing has occurred in some of these lines in the recent past.

Table 30. -- Expected segregation, on the basis of parental traits, for qualitative traits in F_2 lines

Cross	Stem color	Calyx color	Flower color	Pod color	Wing color	Pod shape
HV1 x PB5a	-	-	-	-	-	-
PB3 x PV5	s	-	-	-	-	-
PB3 x PW	s	-	s	-	-	s
PB5b x UP7c	?	s	s	-	?	s
PV5 x PB5a	-	-	-	-	-	-
PV5 x UV1-a	s	s	-	-	s	-
PV5 x UV1-b	s	s	-	-	s	-
UB3a x HV1	s	s	-	-	s	s
UGM x PB1b	-	-	s	-	-	-
UGM x UB3b	s	s	-	s	?	s
UR2b x PB1b	?	s	s	s	?	-
UV1 x PV5	s	s	-	-	s	-
UV5 x UP3b	?	s	s	-	?	s

s = segregation expected in F_2
- = no segregation expected in F_2
? = trait of one parent not recorded
[z]selfs from Table 7 excluded

Table 31. -- Segregation and lack of segregation for qualitative traits in F_2 lines[z]

Cross	Stem color	Calyx color	Flower color	Pod color	Wing color	Pod shape
HV1 x PB5a	-	-	-	-	-	-
PB3 x PV5	s	-	-	s[y]	-	-
PB3 x PW	l	-	s	-	-	s
PB5b x UP7c	-[x]	s	s	-	s[x]	s
PV5 x PB5a	s[y]	-	-	-	-	-
PV5 x UV1-a	s	s	-	-	s	-
PV5 x UV1-b	s	s	-	-	s	-
UB3a x HV1	s	s	-	s[y]	s	s
UGM x PB1b	-	-	s	-	-	-
UGM x UB3b	s	s	-	s	s[x]	l
UR2b x PB1b	s[x]	s	s	s	s[x]	-
UV1 x PV5	s	s	-	-	s	-
UV5 x UP3b	-[x]	s	s	s[y]	s[x]	s

s = segregation in F_2
- = no segregation found or expected in F_2
l = lack of expected segregation in F_2

[z] selfs from Table 7 excluded

[y] parents don't differ for trait

[x] trait of one parent not recorded

Table 32. -- Results for stem, calyx and flower color

Cross	Stem color[z]			Calyx color[y]				Flower color[x]			
	F_1	F_2 p	F_2 g	F_1	F_2 g	F_2 pg	F_2 p	F_1	F_2 vb	F_2 w	F_2 rp
HV1 x PB5a	g	4[w]	54	g	58	-	-	vb	58	-	-
PB3 x PV5	g	35	43	g	77	1[w]	-	vb	78	-	-
PB3 x PW	g	-	90	g	82	7[w]	-	w	19	69	-
PB5b x UP7c	g	5[w]	123	p	28	4	96	rp	28	-	97
PV5 x PB5a	g	21	52	g	73	-	-	vb	73	-	-
PV5 x UV1-a	g	53	62	g	87	27	2[w]	vb	116	-	-
PV5 x UV1-b	g	20	18	g	33	4	1[w]	vb	38	-	-
UB3a x HV1	p	50	32	pg	40	37	6	vb	81	-	-
UGM x PB1b	g	4[w]	87	g	82	4[w]	5[w]	w	23	56	5[w]
UGM x UB3b	p	80	43	g	53	49	21	vb	107	8[w]	2[w]
UR2b x PB1b	p	30	27	g	35	14	8	w	24	27	3[w]
UV1 x PV5	g(?)	35	13	g	34	13	1[w]	vb	45	1[w]	1[w]
UV5 x UP3b	g	2[w]	115	p	23	2	84	rp	24	1[w]	84

[z]p = purple, g = green; [y]g = green, pg = purple-green, p = purple
[x]vb = violet-blue, w = white, rp = red-purple; [w]off-type character

Table 33. -- Results for pod and wing color and pod shape

Cross	Pod color[z]			Wing color[z]			Pod shape[y]		
	F_1	F_2 g	F_2 p	F_1	F_2 g	F_2 p	F_1	F_2 r	F_2 f
HV1 x PB5a	g	57	-	g	57	-	r	57	-
PB3 x PV5	g	51	25	g	75	1[x]	r	75	-
PB3 x PW	g	90	-	g	85	5[x]	r	53	36
PB5b x UP7c	g	113	14[x]	p	60	67	r	101	26
PV5 x PB5a	g	73	-	g	73	-	r	73	-
PV5 x UV1-a	g	107	4[x]	g	80	31	r	111	-
PV5 x UV1-b	g	36	-	g	31	5	r	36	-
UB3a x HV1		46	38	g	62	22	r	61	23
UGM x PB1b	g	91	-	g	86	5[x]	r	91	-
UGM x UB3b	g	84	32	g	75	41	r	118	-
UR2b x PB1b	g	49	6	g	41	14	r	55	-
UV1 x PV5	g	47	1[x]	g	36	12	r	48	-
UV5 x UP3b	g	38	44	p	23	58	r	59	21

[z] g = green, p = purpling

[y] r = rectangular cross-section, f = flat

[x] off-type character

Expression of off-type characters can be used as an indicator of detectable outcrossing. The percentage of detectable outcrossing as measured by off-types ranged from 0 to 24.6% (Table 34). Much of the variability in outcrossing percentage was due to the criteria used for picking out off-type plants. Selfs, which had available as criteria every trait recorded, had 4 out of the 5 populations with the highest percentage of off-types, but this was mostly due to stem color. When stem color was excluded, very low levels of outcrossing were detected in these (Table 35). Stem color accounting for an inordinate amount of detectable outcrossing brings up the question of whether it is a valid measure of outcrossing. There are several reasons to expect stem color to show up in more off-types than the other traits. First, one would not expect recessive traits such as flat pods to show up as off-types. Secondly, there were more more purple stemmed plants in the field populations than plants having other off-type traits. The majority of plants were violet-blue flowered, green, rectangular podded plants. Thus, there was a greater probability of a bee visiting a purple stemmed plant than visiting a plant with purple calyxes, speckled pods or red-purple flowers.

Since off-type plants are identified by differences from both parents in one or more of the recorded traits, insect outcrossing to a line or plant not differing in the

Table 34. -- Frequency of off-type plants in F_2 populations

Cross	Criteria for off-types[z]	Off-types	(%)	Date[y]
PV5 x UB3a[x]	stem-p	17/69	24.6	11/81
HV1 x PW[x]	stem-p, pod shape-f	15/73	20.5	11/81
PB5a x PW[x]	stem-p, cal-pg, pod-p flcol-w	12/66	18.2	11/81
PB5b x UP7c	stem-p, cal-pg, pod-p	22/128	17.2	4/82
HV1 x UW2[x]	stem-p, pod-p	5/40	12.5	11/81
UGM x PB1b	stem-p, cal-pg/p, pod-p wing-p, flcol-rp	10/91	11.0	4/82
UV1 x PV5	pod-p, flcol-rp/w, pod shape	4/48	8.3	9/82
UGM x UB3b	flcol-non vb	10/123	8.1	4/82
PB3 x PW	stem-p, cal-p/pg, pod-p wing-p	7/90	7.8	11/81
HV1 x PB5a[w]	stem-p	4/58	6.9	11/81
PV5 x UP3a[x]	stem-p, pod shape-f	4/74	5.4	11/81
UR2b x PB1b	flcol-rp, pod shape-f	3/57	5.3	4/82
PV5 x UV1-a	pod-p, flcol-non vb pod shape-f, cal-p	5/116	4.3	9/82
UV5 x UP3b	flcol-w, stem-p, cal-pg	5/117	4.3	4/82
PV5 x UW2[x]	stem-p, pod shape	3/77	3.9	11/81

See footnotes on next page

Table 34. (cont.). Frequency of off-type plants in F_2 populations

Cross	Criteria for off-types[z]	Off-types	(%)	Date[y]
PV5 x UV1-b	pod-p, flcol-non vb, cal-p	1/38	2.6	9/82
PB3 x PV5	cal-pg/p, wing-p flcol-non vb	2/78	2.6	11/81
PV5 x PB5a	cal-pg/p, pod-p, wing-p, flcol-non vb, pod shape	0/73	0	11/81
UB3a x HV1	flcol-non vb	0/82	0	11/81

[z] p = purple, f = flat, cal = calyx, pg = purple-green, flcol = flower color, rp = red-purple, w = white, vb = violet-blue

[y] date of planting of F_1 parent of F_2

[x] apparent selfs

[w] no differentiating traits between parents

note: selfs and crosses with no differentiating traits have listed under criteria only those traits found as off-types; other lines have listed as criteria all traits not found in either parent

Table 35. -- Frequency of off-type plants in F_2 with stem purpling excluded[z]

Cross	Criteria for Off-types[y]	Off-types	(%)	Date[x]
PB5b x UP7c	pod-p, calyx-pg	18/128	14.1	4/82
UGM x PB1b	calyx-pg/p, wing-p flcol-rp	9/91	9.9	4/82
UV1 x PV5	pod-p, flcol-non vb	4/48	8.3	9/82
UGM x UB3b	flcol - non vb	10/123	8.1	4/82
PB3 x PW	calyx-p/pg, pod-p, wing-p	7/90	7.8	11/81
PB5a x PW[w]	calyx-pg, flcol-w, pod-p	4/66	6.1	11/81
UR2b x PB1b	flcol-rp, pod shape-f	3/57	5.3	4/82
PV5 x UV1-a	pod-p, flcol-non vb	5/116	4.3	9/82
PV5 x UP3a[w]	pod shape-f	2/74	2.7	11/81
HV1 x UW2[w]	pod-p	1/40	2.5	11/81
UV5 x UP3b	calyx-pg, pod-p	2/117	1.7	4/82
HV1 x PW[w]	pod shape-f	1/73	1.4	11/81
HV1 x PB5a[v]		0/58	0	11/81
PV5 x UB3a[w]		0/69	0	11/81
PV5 x UW2[w]		0/77	0	11/81

[z]only lines showing outcrossing percentage of over 3% in Table 34 included

[y]p = purple, f = flat, cal = calyx, pg = purple-green, flcol = flower color, rp = red-purple, w = white, vb = violet-blue

[x]date of planting of F_1 parent of F_2

[w]apparent selfs

[v]no differentiating traits between parents

traits used as off-type criteria would not be identifiable. Thus, total outcrossing will tend to be underestimated to varying degrees.

The F_2 data will be discussed character by character with the off-type plants excluded in order to see if some coherent patterns emerge.

1. Stem Color

Six crosses, that were expected on the basis of parental traits to show segregation for stem color, did in fact segregate (Table 30). Two crosses in which the stem color of one of the parents was not recorded also showed segregation for this character. One cross, PV5 x PB5a, in which the parents didn't differ for stem color seemed to be showing segregation for this trait. One cross, PB3 x PW, which should have segregated for stem color did not.

Both my F_1 results and the findings of Erskine and Khan (1977) seem to indicate that purple is dominant to green stem. Thus, more purple than green F_2 progeny are expected from purple stemmed F_1's. This was the case for UB3a x HV1, UGM x UB3b, UR2b x PB1b (Table 32). For UV1 x PV5, the F_1 was recorded as green, but as discussed earlier, this may have been a mistake. The F_2 results for UV1 x PV5 are consistent with a purple stemmed F_1. When these lines are tested for fit to genetic ratios using the data adjusted to exclude observable off-type plants, only UGM x UB3b and

UV1 x PV5 have acceptable chi-squares for a 3:1 ratio of purple:green (Table 36). Testing for a 9:7 ratio of purple to green, which is indicative of complementary gene action, PV5 x UV1-b, UB3a x HV1 and UR2b x PB1b had good chi-squares for fit (Table 37). However, PV5 x UV1-b and UR2 x PB1b also would fit a 9:7 ratio of green:purple (Table 38). In addition, PV5 x UV1-a and PB3 x PV5 fit a 9:7 ratio of green:purple. Of these 4 F_2 lines, three of these had green F_1's. There is an obvious discrepancy between UV1 x PV5 and its 2 reciprocals. Maternal cytoplasmic effects on inheritance and heterozygosity in a parent for stem color are possible partial explanations, although neither is satisfactory.

Another line, PV5 x PB5a derives from a green stemmed F_1 from 2 green stemmed parents, and yet sizeable portions of the F_2's are purple stemmed. A possible explanation for this line is that the segregation is not genetic but is due to a high degree of outcrossing. However, for all other characters in this line the amount of discernible outcrossing is minimal.

Thus, the apparent indication by the F_1 results of dominance of purple to green is not supported by the F_2 data, which does not make a lot of sense. With the possible high degree of outcrossing and the problems in classification, it is not possible to make any conclusions about stem color on the basis of the F_2 data.

Table 36. -- Stem color - fitting F_2 lines to a 3:1 genetic ratio of purple:green

Cross	Observed	Expected	Chi-square
	p:g	p:g[z]	
UGM x UB3b[y]	76:37	84.75:28.25	3.212
UV1 x PV5[y]	32:12	33:11	0.030
PV5 x UV1-a[y]	48:62	82.5:27.5	56.048***
PV5 x UV1-b	19:18	27.75:9.25	9.811**
UB3a x HV1	50:32	61.5:20.5	7.870**
UR2b x PB1b[y]	28:26	40.5:13.5	14.222**

*significant at 5% level
**significant at 1% level
***significant at .1% level
[z]p = purple, g = green
[y]after off-type plants excluded from data

Table 37. -- Stem color - fitting F_2 lines to a 9:7 genetic ratio of purple:green

Cross	Observed	Expected	Chi-square
	p:g	p:g[z]	
PV5 x UV1-b[y]	19:18	20.812:16.187	0.189
UB3a x HV1	50:32	46.125:35.875	0.564
UR2b x PB1b[y]	28:26	30.375:23.625	0.264
PB3 x PV5[y]	33:43	42.75:33.25	4.575*
PV5 x UV1-a[y]	48:62	61.875:48.125	6.608*
UGM x UB3b[y]	76:37	63.56:49.44	5.124*
UV1 x PV5[y]	32:12	24.75:19.25	4.208*

*significant at 5% level
**significant at 1% level
***significant at 0.1% level
[z]p = purple, g = green
[y]after off-type plants excluded from data

Table 38. -- Stem color - fitting F_2 lines to a 9:7 genetic ratio of green:purple

Cross	Observed g:p	Exp. numbers p:g[z]	chi-square
PB3 x PV5[y]	43:33	42.75:33.25	0.000
PV5 x UV1-a[y]	62:48	61.875:48.125	0.000
PV5 x UV1-b[y]	18:19	20.8125:16.1875	0.587
UR2b x PB1b[y]	26:28	30.375:23.625	1.130
PV5 x PB5a	52:21	41.0625:31.9375	6.064*
UB3a x HV1	32:50	46.125:35.875	9.199**
UGM x UB3b[y]	37:76	63.5625:49.4375	24.426***

*significant at 5% level
**significant at 1% level
***significant at0.1% level

[z]p = purple, g = green
[y]after off-type plants excluded from data

2. Calyx Color

There are 8 crosses which are expected to show segregation for this trait (Table 30). All appear to be segregating for calyx color, 5 crosses showing segregation into only 2 classes and the other 3 being distributed over all 3 classes (Table 32).

The F_1 data for purple-green calyx UV1 crossed with green calyx PV5 showed dominance of green to purple-green, so we expect more green than purple-green progeny in the F_2. The F_2 confirmed this with a 3:1 ratio of green:purple-green (Table 39). However, the other purple-green by green calyx cross, UGM x UB3b gave both purple-green and green calyxes in the F_1 and the progeny of the green calyx F_1 showed distribution over all 3 classes in the F_2.

Crosses between green and purple calyx parents gave overall F_1 results difficult to interpret. Erskine and Khan (1977) reported purple dominant to green, with one major gene controlling the segregation. Two lines grown out from purple calyx F_1's, PB5b x UP7c and UV5 x UP3b, supported this (Table 40). The other 2 crosses between green and purple parents, UB3a x HV1 and UR2b x PB1b, which were from purple green and green F_1's, respectively, gave F_2 progeny distributed over all 3 classes (Table 32).

Table 39. -- Crosses between green and purple-green calyx parents - fitting F_2 lines to a 3:1 genetic ratio of green:purple-green

Cross	Observed	Expected	Chi-square[z]
	g:pg	g:pg[y]	
PV5 x UV1-a[x]	85:26	83.25:27.75	1.619
PV5 x UV1-b	33:4	27.75:9.25	3.252
UV1 x PV5[x]	33:11	33:11	0

[z]all chi-square values non-significant
[y]g= green, pg = purple green
[x]after off-type plants excluded from data

Table 40. -- Crosses between green and purple calyx parents - fitting F_2 lines to a 1:3 genetic ratio of green:purple

Cross	Observed	Expected	Chi-square[z]
	g:p	g:p[y]	
PB5b x UP7c[x]	24:82	26.5:79.5	0.201
UV5 x UP3b[x]	22:82	26:78	0.628

[z]chi-square values non-significant
[y]g = green, p = purple
[x]after off-type plants excluded from data

3. Flower Color

Five crosses were expected to segregate for flower color. Lines PB5b x UP7c and UV5 x UP3b segregated into red-purple and violet-blue flowers and PB3 x PW and UGM x PB1b segregated for white and violet-blue, as expected. Cross UR2b x PB1b was expected to segregate for white and red-violet, but showed segregation for violet-blue and white. There is not sufficient information to explain this.

The F_1 data indicated that red-purple and white are both dominant to violet-blue. The F_2 results supported this, giving a 3:1 ratio of red-purple to violet-blue for PB5b x UP7c and UV5 x UP3b (Table 41) and a 3:1 ratio of white to violet-blue for PB3 x PW and UGM x PB1b (Table 42). Thus, flower color in each of these cases appears to be controlled by differences of one major gene. However, the anomalous UR2b x PB1b did not fit a 3:1 ratio.

There was a strong correlation of red-purple flowers with purple calyxes. All the parents and F_1's with red-purple flowers also had purple calyxes, although the obverse was not so. In the F_2's of PB5b x UP7c, 96 of the 97 red-purple flowered plants had purple calyxes, and 84 of 84 red-purple flower UV5 x UP3b F_2's had purple calyxes. Crosses involving purple calyx and non-red-purple flower parents did not show this relationship. Thus, purple calyx color is closely linked to red-purple flower color.

Table 41. -- Winged bean flower color - fitting F_2 lines to a 3:1 genetic ratio of red-purple:violet-blue

Cross	Observed	Expected	Chi-square[z]
	rp:vb	rp:vb[y]	
UV5 x UP3b[x]	82:22	78:26	0.628
PB5b x UP7c[x]	81:23	78:26	0.321

[z]all chi-square values non-significant
[y]rp = red-purple, vb = violet-blue
[x]after off-type plants excluded from data

Table 42. -- Winged bean flower color - fitting F_2 lines to a 3:1 ratio of white:violet-blue

Cross	Observed	Expected	Chi-square[z]
	w:vb	w:vb[y]	
PB3 x PW	69:19	66:22	0.424
PB3 x PW[x]	69:12	60.75:20.25	3.955*
UGM x PB1b[x]	54:20	55.5:18.5	0.018
UR2b x PB1b	27:24	38.25:12.75	12.085***

***significant at 0.1% level of probability
[z]chi-square values non-significant unless otherwise noted
[y]w = white, vb = violet-blue
[x]after off-type plants excluded from data

Four F_2 lines had plants with streaked flowers (Table 43) as illustrated in fig. 5. These plants also had uniformly colored and white flowers. Similar phenomena have been explained by transposable genetic elements (Doodeman et.al., 1984; McClintock, 1965).

4. Pod Color

Based on parental characters, genetic segregation for pod color was expected only for UGM x UB3b and UR2b x PB1b (Table 30). Based on the dominance expressed in the F_1 for green in these 2 crosses, more green than purple F_2 progeny were expected. Line UGM x UB3b fit a 3:1 ratio of green to purple, but UR2b x PB1b did not (Table 44).

Three other F_2's appear to be segregating for this trait. Line PB3 x PV5 fits a one gene ratio of 3:1 green to purple. Lines UB3a x HV1 and UV5 x UP3b will fit a 9:7 ratio (Table 45), although UV5 x UP3b had a large proportion of plants, 35/117, which did not produce pods.

5. Pod Wing Color

Segregation for pod wing color was expected in 4 crosses. In addition there were 4 lines in which the wing color of one parent was not recorded (Table 30). All 8 showed segregation (Table 33).

Six of the lines were derived from green F_1's. As would be expected, there were more green pod wing progeny

Table 43. -- Incidence of streaking in winged bean flowers in F_2 generation

Cross	Flower colors	Number of plants With streaked flowers	% of pop.
PB3 x PW	w/vb	1	1.11
PB5b x UP7c	w/rp	3	2.34
UGM x UB3b	w/vb	6	4.88
UR2b x PB1b	w/vb	3	5.26
UGM x PB1b	w/vb	7	7.69

[z]w = white, rp = red-purple, vb = violet-blue

Figure 5. Color streaking in winged bean flowers

Table 44. -- Pod color - fitting F_2 lines to a 3:1 genetic ratio of green:purple

Cross	Observed	Expected	Chi-square[z]
	g:p	g:p[y]	
UGM x UB3b[x]	76:30	79.5:26.5	0.453
PB3 x PV5[x]	50:24	55.5:18.5	1.802
UR2b x PB1b	46:6	39:13	4.333*
UB3a x HV1	46:38	63:21	17.286***
UV5 x UP3b[x]	35:43	58.5:19.5	36.171***

*significant at 5% level
***significant at 0.1% level
[z]chi-square values non-significant unless otherwise noted
[y]g = green, p = purple
[x]after off-type plants deleted from data

Table 45. -- Pod color - fitting F_2 lines to a 9:7 genetic ratio of green:purple

Cross	Observed	Expected	Chi-square
	g:p	g:p[z]	
UB3a x HV1	46:38	47.25:36.75	0.027
UV5 x UP3b[y]	35:43	43.875:34.125	3.654
PB3 x PV5[y]	50:24	41.625:32.375	3.405
UGM x UB3b[y]	76:30	59.625:46.375	9.661**

**significant at 1% level of probability
[z]g = green, p = purple
[y]after off-type plants deleted from data

than purple winged for all of these. Four lines, including all 3 involving PV5 and UV1, fit a 3:1 ratio of green to purple (Table 46). Line UGM x UB3b didn't fit a one locus ratio, but did fit a 9:7 ratio of green:purple (Table 47). Line PB5b x UP7c, which was from a purple wing F_1, would fit a 9:7 ratio of either green:purple or purple:green.

Cross UV5 x UP3b did not fit with any of the other lines. It also had 35 plants which did not produce pods.

6. Pod Shape

Segregation for pod shape was expected in 3 F_2 lines. In addition, one cross for which the pod shape of the F_1 was not recorded and one parent (UV5) was listed as r ?, showed segregation. Based on the F_1 data, we expect a ratio indicative of dominance of rectangular over flat pod cross-section. Three of the lines fit a 3:1 ratio of rectangular to flat (Table 48) and the other line, PB3 x PW, fit a ratio of 9:7 rectangular:flat (Table 49). The results for the 3:1 ratio of rectangular to flat are in agreement with those of Erskine and Khan (1977) indicating a one major gene difference.

Table 46. -- Pod wing color - fitting F_2 lines to a genetic ratio of 3:1 green:purple

Cross	Observed	Expected	Chi-square
	g:p	g:p[z]	
PV5 x UV1-a[y]	79:27	79.5:26.5	0.00
PV5 x UV1-b[y]	31:4	26.25:8.75	2.836
UV1 x PV5[y]	35:9	33:11	0.273
UB3a x HV1	62:22	63:21	0.016
UR2b x PB1b[y]	41:11	39:13	0.231
UGM x UB3b[y]	67:39	79.5:26.5	7.245**
PB5 x UP7c[y]	52:54	79.5:26.5	36.679***

**significant at 1% level
***significant at 0.1% level
[z]g = green, p = purple
[y]after off-type plants excluded from data

Table 47. -- Pod wing color - fitting F_2 lines to genetic ratio of 9:7 green:purple

Cross	Observed	Expected	Chi-square
	g:p	g:p[z]	
UGM x UB3b[y]	67:39	59.625:46.375	1.479
PB5b x UP7c[y]	52:54	59.625:46.375	1.946
PV5 x UV1-a[y]	79:27	59.625:46.375	13.657***
PV5 x UV1-b[y]	31:4	20.25:15.75	13.573***
UV1 x PV5[y]	35:9	24.75:19.25	8.779**
UB3a x HV1	62:22	47.25:36.75	5.526*
UR2b x PB1b[y]	41:11	29.25:22.75	9.890**
UV5 x UP3b[y]	21:56	43.312:33.688	25.108***

*significant at 5% level
**significant at 1% level
***significant at 0.1% level
[z]g = green, p = purple
[y]after off-type plants excluded from data

Table 48. -- Cross-sectional pod shape - fitting F_2 lines to a 3:1 ratio of rectangular:flat

Cross	Observed	Expected	Chi-square
	r:f	r:f[z]	
PB5b x UP7c[y]	84:22	79.5:26.5	0.744
UV5 x UP3b[y]	55:21	57:19	0.158
UB3a x HV1	61:23	63:21	0.141
PB3 x PW[y]	51:31	61.5:20.5	6.504*

*significant at 5% level of probability
[z]r = rectangular, f = flat
[y]after off-type plants excluded from data

Table 49. -- Cross-sectional pod shape - fitting F_2 lines to a 9:7 ratio of rectangular:flat

Cross	Observed	Expected	Chi-square
	r:f	r:f[z]	
PB3 x PW[y]	51:31	46.125:35.875	0.948
PB5b x UP7c[y]	84:22	59.625:46.375	21.851***
UV5 x UP3b[y]	55:21	42.75:33.25	7.382**
UB3a x HV1	61:23	47.25:36.75	8.493**

**significant at 1% level of probability
***significant at 0.1% level of probability
[z]r = rectangular, f = flat
[y]after off-type plants excluded from data

SUMMARY AND GENERAL DISCUSSION

Determining the inheritance of pigmentation and pod shape in winged bean proved more difficult than anticipated. The assumption that outcrossing was negligible in winged bean, (made on the basis of reports by Aminah-Lubis, 1978 and Erskine, 1980), proved to be incorrect. In conjunction with this, many of the parents, initially assumed to be homozygous, turned out to be heterozygous for one or more of the characters evaluated. Likewise, many plants in the F_2 generation were off-types, presumably from outcrossing. Even though outcrossed progeny were not always identifiable as such, some progenies had as much as 25% off-types, and it would not be unreasonable to assume that outcrossing was high, although variable, for the population in general.

In spite of the lack of homozygosity in some parents, the dominance or recessiveness of a trait in the F_1 should be identifiable. In the F_2, at least one half of the F_2 progeny from a heterozygous F_1 parent should express the dominant trait regardless of outcrossing, if the trait is controlled by one locus. With more than 1 locus and interaction, it would be possible to have less than half the progeny expressing the dominant trait.

Therefore, if these characters are controlled by one locus as reported by Erskine and Khan (1978), tentative conclusions should be possible from my results.

Generally, the dominance of purple to green stem color as reported by Erskine and Khan (1977) was confirmed by the F_1 results. The F_2's of the 3 purple stemmed F_1's and that of UV1 x PV5 were in accord with the dominance of purple to green. The progeny of the green stemmed F_1's would not be expected to show segregation for stem color, but some did. Three F_2 populations derived from green F_1's had a good fit for a 9:7 ratio of green:purple. Further complicating this is the contradictions between UV1 x PV5 and its' reciprocols.

Calyx color was classified into 3 phenotypes in this study, green, purple-green, and purple, unlike Erskine and Khan who had only purple and green classes. Segregation in crosses between purple and green parents supported the finding of Erskine and Khan that purple is dominant. The purple-green phenotype was recessive to green. Some crosses segregated into all 3 classes, but these results were not consistent.

The only reference to inheritance of flower color in winged bean stated that white is recessive to other colors (Sastrapradja et al., 1980). The F_1 results in this study did not bear this out, except in crosses with UB3. In 7 other crosses of white by violet-blue, the F_1 was always white. Red-purple flower color was dominant to white, as well as all the other colors. Red-violet was not expressed in the F_1 or F_2 generations.

Erskine and Khan reported that purple speckling of pods is dominant to green. The dominance of purpling was confirmed in crosses with PR3, which had pods which progress from purple speckling to dark red purple. In crosses with UR2 and UB3, in which the pods remain speckled, green was dominant to purple speckling. The F_2 results were variable and there may be some environmental-genotypic interaction involved in expression of pod purpling.

Erskine and Khan also reported that purple pod wing is dominant to green. However, 5 of 7 F_1's between purple and green pod wing parents were green, and 7 of 8 F_2's had more green than purple wing plants. These results tend to conflict with the findings of Erskine and Khan.

Erskine and Khan also reported that rectangular pod shape was dominant to flat. The results from the present study agree with this hypothesis.

Erskine and Khan (1977) are the only workers who have reported on the inheritance of these characters in winged bean. However, their study was based on only 2 crosses between 3 parents, all of Papua New Guinea origin, none of which were used in the present study. My results agreed with theirs only for pod shape. For all of the other characters, some results agreed and others did not. Thus, it seems likely that there is more variability in winged bean than that reported by Erskine and Khan from their 2 crosses.

The results obtained in this study are frequently contradictory and ambiguous. While many of the inconsistencies can be attributed to outcrossing, it is possible some are due to environmental factors, the classification system, different genetic factors in different lines, or even mislabeling and seed mixture. In order to determine the inheritance of these or other traits in winged bean, it would be necessary to ensure that all variables, especially the possibility of insect outcrossing, are controlled as much as possible.

Firstly, parental lines should be selfed until homozygous for the traits under study. These lines should be chosen to represent a diverse range of characteristics found to exist in winged bean, including those with differing results in the present study. Since open-pollinated flowers are often insect cross-pollinated, selfing can be done by bagging individual flowers, caging plants, or spatial and temporal isolation.

When the parents are apparently homozygous for the traits under study, they will be used in crosses. The crosses will be bagged at time of emasculation and rebagged after pollination. Pollen contamination will be prevented by bagging buds before they open or by growing the crossing blocks in a bee-free greenhouse. Two feasible possibilities for crossing combinations are 6 parents, each crossed to 2 common tester lines, and the 2 tester lines crossed giving

13 crosses or else a half diallel with 6 parents. The half diallel would involve 15 crosses. Multiple pollinations need to be made on each plant in order to have an adequate number of F_1 plants for analysis of quantitatively inherited traits.

The resulting F_1 seed would be used as follows. Some would be saved for later planting in conjunction with F_2's, parental lines, and backcrosses. A few seeds from each cross, e.g. 10, would be grown out to check for variability in the F_1, for selfing, and to backcross to both parents. Backcross information is needed to partition genetic variability into additive and non-additive components.

The last stage will be plantings of the F_2, F_1, parental and backcross lines for data collection. Fifteen plants each of the F_1 and parental lines and 100 plants of each backcross and F_2 should give sufficient genetic information. Hopefully, by controlling the source of pollen in each instance, the ambiguities and inconsistencies in this study can be resolved.

APPENDIX

Table 50. -- Information on parental traits on a cross by cross basis

Crosses with F_2 progeny[z]

Cross	Stem color[y]	Calyx color[x]	Flower color[w]	Pod color[y]	Wing color[y]	Pod shape[v]
HV1 x PB5a	g x g	g x g	vb x vb	g x g	g x g	r x r
HV1 x PW[s]	g x g	g x g	vb x w	g x g	g x g	r x f
HV1 x UW2[s]	g x g	g x g	vb x w	g x g	g x g	r x f
PB3 x PV5	p x g	g x g	vb x vb	g x g	g x g	r x r
PB3 x PW	p x g	g x g	vb x w	g x g	g x g	r x f
PB5b x UP7c	g x	g x p	vb x rp	g x g	g x	r x f
PB5a x PW[s]	g x g	g x g	vb x w	g x g	g x g	r x f
PV5 x PB5a	g x g	g x g	vb x vb	g x g	g x g	r x r
PV5 x UB3a[s]	g x p	g x p	vb x vb	g x g	g x p	r x f
PV5 x UP3a[s]	g x p	g x p	vb x rp	g x g	g x p	r x r
PV5 x UV1	g x p	g x pg	vb x vb	g x g	g x p	r x r
PV5 x UW2[s]	g x g	g x g	vb x w	g x g	g x g	r x f
UB3a x HV1	p x g	p x g	vb x vb	g x g	p x g	f x r
UV1 x PV5	p x g	pg x g	vb x vb	g x g	p x g	r x r
UGM x PB1b	g x g	g x g	vb x w	g x g	g x g	r x r
UGM x UB3b	g x p	g x gp	vb x vb	g x p	g x	r x f
UR2b x PB1b	x g	p x g	rv x w	p x g	x g	r x r
UV5 x UP3b		g x p	vb x rp	g x g	x p	x r

Table 50. (cont.). Information on parental traits on a cross by cross basis

Crosses without F_2 progeny[z]

Cross	Stem color[y]	Calyx color[x]	Flower color[w]	Pod color[y]	Wing color[y]	Pod shape[v]
HV1 x PR3b	g x p	g x p	vb x rv	g x p	g x p	r x r
HV1 x PR3c	g x p	g x p	vb x rv	g x p	g x p	r x r
HV1 x UGM	g x g	g x g	vb x vb	g x g	g x g	r x r
HV1 x UP3c[u]	g x g	g x p	vb x rp	g x g	g x g	r x r
HV1 x UW2	g x g	g x g	vb x w	g x g	g x g	r x f
PB1a x HV1	g x g	g x g	vb x vb	g x g	g x g	r x r
PB1a x UW2	g x g	g x g	vb x w	g x g	g x g	r x f
PB3 x HV1	p x g	g x g	vb x vb	g x g	g x g	r x r
PB3 x PB1a	p x g	g x g	vb x vb	g x g	g x g	r x r
PB3 x PB5a[u]	p x g	g x g	vb x vb	g x g	g x g	r x r
PB3 x UB3a	p x p	g x p	vb x vb	g x g	g x p	r x f
PB3 x UR2a	p x p	g x p	vb x rv	g x p	g x p	r x r
PB3 x UW2	p x g	g x g	vb x w	g x g	g x g	r x f
PB5a x HV1	g x g	g x g	vb x vb	g x g	g x g	r x r
PB5b x UP7b	g x	g x p	vb x rp	g x g	g x	r x f
PV5 x HV1	g x g	g x g	vb x vb	g x g	g x g	r x r
PV5 x PB1a	g x g	g x g	vb x vb	g x g	g x g	r x r
PV5 x PB3	g x p	g x g	vb x vb	g x g	g x g	r x r
PV9 x UB3a	p x p	g x p	vb x vb	g x g	g x p	r x f

See footnotes on next page

Table 50. (cont.). Information on parental traits on a cross by cross basis[z]

Crosses without F_2 progeny[z]

Cross	Stem color[y]	Calyx color[x]	Flower color[w]	Pod color[v]	Wing color[y]	Pod shape[u]
PW x HV1	g x g	g x g	w x vb	g x g	g x g	f x r
PW x PB1a	g x g	g x g	w x vb	g x g	g x g	f x r
PW x PB3	g x p	g x g	w x vb	g x g	g x g	f x r
PW x UB3a	g x p	g x p	w x vb	g x g	g x p	f x f
PW x UW2	g x g	g x g	w x w	g x g	g x g	f x f
UGM x HV1	g x g	g x g	vb x vb	g x g	g x g	r x r
UGM x UB3c	g x p	g x pg	vb x vb	g x p	g x	r x f
UGM x UP3d[u]	g x g	g x p	vb x rp	g x g	g x g	r x r
UGM x UR2d	g x	g x p	vb x rv	g x p	g x	r x r
UP7d x UR2c		p x pg	rp x vb	g x p		f x r
UP7e x UR2c		p x pg	rp x vb	g x p		f x r
UV1 x PR3b	p x p	pg x p	vb x rv	g x p	p x p	r x r
UW2 x PB5a	g x g	g x g	w x vb	g x g	g x g	f x r
UW2 x UB3a	g x p	g x p	w x vb	g x g	g x p	f x f

[z] maternal parent listed first
[y] g = green, p = purple
[x] g = green, pg = purple-green, p = purple
[w] vb = violet-blue, w = white, rp = red-purple, rv = red-violet
[v] r = rectangular pod cross-section, f = flat pod
[u] contaminated cross
[s] apparent self

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